FOSSIL XENARTHRAN MAMMALS FROM VENEZUELA – TAXONOMY, PATTERNS OF EVOLUTION AND ASSOCIATED FAUNAS

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Zusammenfassung der Dissertation für nichtakademisches Laienpublikum

Basierend auf Analysen neuer Fossilfunde werden in der vorliegenden Studie neue Erkenntnisse zur Evolution der Xenarthra des tropischen Südamerikas vorgestellt. Die Vielfalt der Säugetierformen der letzten 10 Millionen Jahre in Venezuela ist ein Schlüssel zum Verständnis der Faunenbewegungen zwischen Süd-, Mittel- und Nordamerika sowie den karibischen Inseln. Es wurden Vertreter zweier Taxa der Xenarthra untersucht: Faultiere, sowie der durch körperbedeckende „Panzer“ charakterisierten Gürteltiere und Glyptodonten. Einige der neu beschriebenen Fossilien repräsentieren neue Stammeslinien und es wurden neuer Gattungen sowie Arten gefunden, welche aus dem südlichen Südamerika unbekannt sind. Der erste Nachweis des Glyptodonten *Glyptotherium* innerhalb Südamerikas ist ein Indiz für das Vorhandensein von eiszeitlichen „Korridoren“ durch den amerikanischen Kontinent.

Abstract for non-academic audience

This work presents new discoveries and analyses of fossils documenting the evolution of the Xenarthra mammals in the tropical regions of South America. The mammalian diversity of the last 10 million years in the area north of the Orinoco River in Venezuela, is a key area to understand the faunal exchanges with Central and North America and with the Caribbean Islands. Representatives of two clades were investigated: the sloths, and the armadillos and glyptodonts, characterized by having their body covered by an “armour” shell. Some of the new fossils are representatives of new lineages and are described as new genera and species unknown from southern South America. The first documentation for South America of the glyptodont *Glyptotherium* suggests the presence of “corridors” across the American continent formed during the maximum glacial periods.

CONTENTS

Abstract

This work presents new discoveries and analyses of fossils documenting much new about the taxonomy and biogeography of Xenarthra, a diverse group of mostly South American distribution. These studies serve to address major issues about the origin and evolution of mammals in the intertropics. Some extensive areas with sedimentary rocks north of the Orinoco River, at the northern extreme of South America, provide a first glimpse into a mammalian diversity from the Neogene unrecorded in other areas of the continent. Some discoveries are being used to document the importance of northern South America as 'cradle and museum' for many clades, and as the key area to understand the nature of the exchanges with Central and North America during the Great American Biotic Interchange and the faunal exchange with the Caribbean Islands during the Cenozoic.

Representatives of two main clades of xenarthrans were investigated: the Tardigrada, commonly known as sloths and ground sloths, and the Cingulata, including the armadillos, pampatheres and glyptodonts, characterized by having their body covered by an "armour" shell formed by articulated and joined osteoderms.

A new genus of glyptodont is erected, *Boreostemma,* which serves as example of the distinctive nature of the northern South American xenarthran diversity in contrast to the Argentinian one. The Colombian and Venezuelan species of this genus had been previously allocated in a taxon of widespread distribution, but new fossils and a consideration of the anatomy and phylogenetic significance of known materials suggests the existence of a distinct intertropical genus. Anatomical comparisons leading to phylogenetic conclusions in a temporal framework, suggest that the Glyptodontinae arose in the northernmost regions of South America and their arrival to more southerly areas coincided with the desertification in lower latitudes of South America, maybe by an open landscape corridor close to the andean area (in the late Miocene-Pliocene interval).

The presence of *Glyptotherium* is documented in the latest Pleistocene (ca. 14 ka) of Venezuela. The discovery of an otherwise North and Central American genus is of great biogeographical significance, as it suggests the presence of “corridors” that could have formed during the maximum of glacial periods. A similar bidirectional migratory pattern has been proposed for another Cingulata group, the pampatheriids, as well as for a megatherin genus.

Because of taphonomical bias, most Tardigrada taxa treated here are represented by long bones, most frequently femora, and consequently, much new anatomical reference work was needed, as most xenarthran fossil and living taxa have been traditionally diagnosed based on other features of the anatomy. The tardigrade diversity recorded in the Neogene of Venezuela is surprisingly large and comparable to that reached only a few times during their history, including the Late Oligocene of Patagonia, Middle Miocene of Patagonia and Late Miocene of northeastern Argentina.

New remains of several postcranial bones of the tardigrade *Urumaquia robusta* are described, significantly improving the knowledge of the species and its relations to other Megatheriinae, in particular with *Pyramiodontherium* and *Megatheriops*.

The Venezuelan xenarthran fossil localities contain a rich diversity and include very basal tardigrade taxa, the earliest representatives of new lineages, as well as clades not known from the extensively prospected sites of southern South America.

Key Words: South America, Postcranial Anatomy, Biogeography, Great American Biotic Interchange, Miocene, Pliocene, Pleistocene

Zusammenfassung

Basierend auf Analysen neuer Fossilfunde werden in der vorliegenden Studie neue Erkenntnisse zur Taxonomie und Biogeographie der Xenarthra, einer formenreichen Gruppe hauptsächlich südamerikanischer Säugetiere, vorgestellt. Mithilfe der neuen Befunde können wichtige Fragen über die Herkunft und Entwicklung der Mammalia des intertropischen Raumes adressiert werden. Ausgedehnte Areale mit Sedimentgesteinen nördlich des Orinoko, im äussersten Norden Südamerikas, ermöglichen erste Einblicke in eine, aus anderen Bereichen des Kontinents nicht belegte, Diversität von Säugetieren aus dem Neogen. Anhand einiger Befunde wird die Bedeutung des nördlichen Südamerikas als "Wiege und Museum" vieler Taxa sowie als Schlüsselstelle für den Faunenaustausch mit Mittel- und Nordamerika während des „Great American Biotic Interchange“ und den faunistischen Austausch mit den karibischen Inseln dokumentiert.

Es wurden Vertreter zweier Taxa der Xenarthra untersucht: Vertreter der Tardigrada (Faultiere), sowie Vertreter der durch körperbedeckende Panzerschalen aus gelenkig verbundenen Osteodermen charakterisierten Cingulata (einschließlich der Gürteltiere und Glyptodonten).

Eine neue Gattung von Glyptodonten, *Boreostemma*, wird errichtet, welche als Beispiel für die besondere Natur der Xenarthren des nördlichen Südamerikas - im Gegensatz zu den argentinischen Formen - dient. Die kolumbianischen und venezolanischen Vertreter dieser Gattung waren zuvor in einem Taxon mit überregionaler Verbreitung zusammengefasst, aber neue Fossilien sowie die Überprüfung der Anatomie und der phylogenetischen Beziehungen des bisher bekannten Fossilmaterials weisen auf die Existenz einer gesonderten, intertropischen Gattung hin. In einem zeitlichen Rahmen eingebettete, auf vergleichend-anatomischen Untersuchungen basierende phylogenetische Schlussfolgerungen deuten darauf hin, dass die Glyptodontinae sich in den nördlichsten Regionen von Südamerika entwickelten, und dass ihre Ankunft in den

südlicheren Bereichen Südamerikas zeitlich mit einer Wüstenbildung in den niederen Breiten korreliert war.

Die Anwesenheit von *Glyptotherium* ist bis ins späteste Pleistozän (ca. 14 ka) Venezuelas dokumentiert. Der Fund einer ansonsten nord- und mittelamerikanischen Gattung ist von großer biogeografischer Bedeutung, da sie das Vorhandensein von "Korridoren", die sich während der Eiszeit gebildet haben könnten, vermuten lässt. Ein ähnlich bidirektionales Migrationsmuster wurde bereits für eine weitere Gruppe der Cingulata, die Pampatheriiden, vorgeschlagen.

Aufgrund taphonomischer Einflüsse sind der Grossteil der in dieser Studie behandelten Taxa durch Langknochen, am häufigsten durch Femora, vertreten. Da die meisten fossilen und heute lebenden Vertreter der Xenarthra traditionell auf der Grundlage anderer anatomischer Eigenschaften diagnostiziert werden, war aufwändige anatomische Referenzarbeit erforderlich. Die Diversität der Tardigrada im Neogen Venezuelas ist erstaunlich hoch. Eine vergleichbare Vielfalt wurde andernfalls nur einige Male, speziell im späten Oligozän sowie im mittleren Miozän von Patagonien und im späten Miozän im nordöstlichen Argentinien, erreicht.

Neue Überreste mehrerer postkranialer Elemente des Tardigraden *Urumaquia robusta* werden beschrieben, welche erheblich zur Verbesserung der Kenntnisse dieser Art und ihrer Beziehungen zu anderen Megatheriinae, insbesondere *Pyramiodontherium* und *Megatheriops*, beitragen.

Die venezolanischen Fundstellen fossiler Xenarthra enthalten eine reiche Diversität an Arten sowie sehr basale Taxa der Tardigrada. Zu diesen gehören die frühesten Vertreter neuer Linien ebenso wie Taxa, welche nicht aus den umfassend bearbeiteten Fundstellen des südlichen Südamerikas bekannt sind.

Key Words: Südamerika, postkraniale Anatomie, Biogeographie, Great American Biotic Interchange, Miozän, Pliozän, Pleistozän

Foreword

The land mammal fossil record of intertropical South America is meagre and does not reflect the biotic richness that dazzled the 19th century explorers like Humboldt, Darwin and Wallace. However, indirect evidences from evolutionary biology and from the Argentinian fossil record suggest that neotropical mammal diversity was enormous (MacFadden 2006; Madden et al. 2010). Thus, any new fossil record from northern South America, in particular Venezuela given its key geographic position, would provide important evidence to examine the early evolution of neotropical mammals as well as evolutionary trends in that continent (Sánchez-Villagra et al. 2010, Appendix). A savannah-like region containing outcrops of mostly Neogene deposits, distributed in localities in Falcón State in north-western Venezuela (Johnson et al. 2006), has delivered a rich fauna of mammals, in particular xenarthrans, the subject of study in this thesis. An overview of the mammalian fauna and of the fossiliferous area in Venezuela which yields that fauna, is presented in chapter 1 of this thesis.

The living Xenarthra includes sloths, anteaters, and armadillos. This clade has had a long and rich evolutionary history that took place in America during most of the Cenozoic, from the Early Paleocene to the present (Carlini et al. 2005, 2010). Their current diversity (about 31 species) does not reflect the remarkable diversity that they reached in the past, with more than 400 species in about 160 genera (McKenna and Bell 1997). The origin of this clade was quite probably in America, although fossil forms have also been found in Eocene sediments of Antarctica, from the time when the latter continent was connected to southern South America (Carlini et al. 1990). A major division within the Xenarthra used in this thesis distinguishes two clades. Those forms with a fur cover are the Pilosa (pilosans), comprising the Tardigrada, commonly known as sloths, and the Vermilingua, the anteaters. The second major group is the Cingulata (armadillos and relatives), characterized by having their body covered by an “armour” shell formed by

articulated and joined osteoderms, analogous to the dermal bones present in some reptiles (Krmpotic et al. 2009).

Recent advances in our knowledge of the Cenozoic xenarthrans from Venezuela are starting to address major issues about the evolution of this clade in the intertropics (Carlini et al. 2006a, 2006b). Some extensive areas with sedimentary rocks north of the Orinoco River, at the northern extreme of South America, are providing a first glimpse into a diversity which is likely to provide major insights into evolution in the continent. Some discoveries are being used to document the importance of northern South America as 'cradle and museum' for some tardigrades and cingulates, and as the key area to understand the nature of the exchanges with Central and North America during the Great American Biotic Interchange and the faunal exchange between the continent and Caribbean Islands. These topics as they relate to cingulate evolution are treated in chapter 2 of this thesis (Carlini and Zurita 2010).

In chapter 3 a new glyptodont genus is erected, *Boreostemma,* which serves as an example of the distinctive nature of the northern South American xenarthran record in contrast to the Argentinian one. The Colombian and Venezuelan species of this genus had been previously allocated in a taxon of widespread distribution, but new fossils and a consideration of the anatomy and phylogenetic significance of known materials suggests the existence of an intertropical genus distinct from Argentinian forms. We postulate that the Glyptodontinae glyptodonts arose in the northernmost regions of South America about 15 Ma or earlier and their arrival to more southerly areas coincided with the acme of the "Age of southern plains", maybe across an open landscape corridor close to the andean area in the late Miocene-Pliocene interval. Moreover, we consider that the new *Boreostemma* species described from the Pliocene of Venezuela, could be very close to the South American species of Gylptodontidae that reached North America at the beginning of the connection between American subplates by the Panamanian isthmus (ca. 2.8 – 2.7 Ma).

Chapter 4 of the thesis documents the presence of *Glyptotherium* in the latest Pleistocene (ca. 14 ka) of Venezuela. The discovery of an otherwise North and Central American genus is of great biogeographical significance, as it suggests the presence of “corridors” that could have formed during the maximum glacial periods. A similar bidirectional migratory pattern has been proposed for another Cingulata group, the pampatheriids, a phenomenon that could have happened as well with the North American Megatheriine genus *Eremotherium*.

The tardigrade xenarthrans treated in this thesis include mylodontoids and megatherioids. Among them are forms closely related to taxa present in the Antilles, Central America and North America. Curiously, because of taphonomic bias, most taxa recognised here are represented by long bones, most frequently femora, and consequently, the initial diagnoses for these taxa have been based on this element (Carlini et al. 2006b, 2006b). Tardigrade diversity recorded for this time period in Venezuela is surprisingly large and comparable to that reached only a few times during their history, including the Late Oligocene of Patagonia (Carlini and Scillato-Yané 2004), Middle Miocene of Patagonia and Late Miocene of the Argentine Mesopotamian, located in the northeast region of that country (Carlini et al. 2001).

In chapter 5 we describe important new remains of the tardigrade *Urumaquia robusta,* described in the context of our first efforts in Venezuela (Carlini et al. 2006b). The new fossils significantly improve the knowledge of the species and allow a more precise discussion about the relationships with the rest of the South American Megatheriinae. The new remains are several postcranial bones exhibiting a several features suggest close affinities of *Urumaquia* with *Pyramiodontherium* and *Megatheriops*, two genera known from more southern latitudes.

In the Appendix the reader finds two of our recent works which illustrate the significance of Venezuela as a source of Cenozoic vertebrate fossils, as well as the potential of new comparative anatomical investigations, such as those on histology of the armour, in revealing new aspects on the palaeobiology of xenarthrans.

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Fossil mammals from the Venezuelan Neogene and the significance of the intertropical record. The Urumaco sequence

Alfredo A. Carlini and Marcelo R. Sánchez-Villagra

Introduction

Recent advances in our knowledge of the Cenozoic vertebrates from Venezuela are starting to address major issues about the origin and evolution of mammalian clades in the intertropics. Some extensive areas with sedimentary rocks north of the Orinoco River, at the northern extreme of South America, are providing a first glimpse into a diversity which is likely to provide major insights into evolution in the continent. Some discoveries are being used to document the importance of northern South America as 'cradle and museum' for many clades, and as the key area to understand the nature of the exchanges with Central and North America during the Great American Biotic Interchange and the faunal exchange between the continent and Caribbean Islands.

At a time in which few studies of fossil vertebrates from Venezuela had been published, Simpson (1940, p. 703-704) stated in his 'Review of the mammal-bearing Tertiary of South America': *'Few as discoveries are, they are important because they show unquestionable affinities with fossil mammals of Argentina and none with those of North America. In view of the fact that no South American mammals had reached North America in the Miocene or earliest Pliocene, even this small budget of evidence is enough to prove that South America was then a unified continent with its northern and southern parts united by land and that the northern part, as well as the southern, was then separated from North America by a marine barrier*'.

More recent discoveries in northern areas of South America (Kay et al. 1997) have indeed confirmed that northern South America has largely speaking the same major clades of mammals documented in the Cenozoic of the higher latitudes of continent, the whole continent having been largely isolated from all others for most of the Cenozoic (Patterson and Pascual 1968, 1972; Pascual, 2006; Reig 1981; MacFadden 2006). But the differences between tropical faunasand those of Argentina are very significant. This is clearly illustrated by the still limited but growing record of fossil mammals from Venezuela.

Several sedimentary basins containing fossil mammals have been recognized north of the Orinoco River. Uplift events ranging in time from latest Eocene until the present, produced sediments that were arranged in molasses cycles (Macsotay et al. 1995). From West to East, orogenic phases produced the Merida Andes, Coastal Range, Eastern Interior, Araya-Paria, and the Northern and Central Ranges of Trinidad. The molasse cycles attained kilometers thickness of sediments. Most relevant in the study of fossil mammals is the Falcon Basin (Fig. 1).

Figure 1. The location in Venezuela of the Falcón sedimentary basin. Modified from Carlini et al. (2008b).

The richest sequence with fossil mammals in the Cenozoic of Venezuela is the Urumaco sequence in the Falcón Basin (Fig. 1). It includes at least four succesive fosiliferous formations, and here we report on the first fossils from a fifth overlaying unit. All other Miocene-Pliocene sites with fossil mammals in Venezuela with vertebrate fossils exhibit very low diversity (Table 1). The richest diversity of fossil mammals from Venezuela is found in Pleistocene tar pit localities recently studied by A. Rincón and colleagues (e.g. 2008), in Quaternary sites of Falcón and Lara States (Aguilera 2006; Sánchez-Villagra et al. 2010), and in numerous caves containing mostly subfossil bats and a few other mammals (Czaplewski et al. 2005; Rincón 2006; Soibelzón and Rincón 2007).

TABLE 1

Formation	Reported age	Location	Reported fossil mammals	References
Castillo Formation	Late Oligocene and Early Miocene	Cerro La Cruz locality, southern flank of the Serranía La Baragua, Lara State		Sánchez-Villagra et al. 2000, 2001, 2004
			Two astrapothere spp., postcranials	Weston et al. 2004
			Sirenian, isolated ribs	Sánchez-Villagra et al. 2004
			Tardigrada indet., isolated teeth.	Sánchez-Villagra et al. 2004
			Cetartiodactyla, Iniidae Gen. et sp. indet., Platanistoidea indet., "Squalodontid" indet., aff. *Prosqualodon australis,* skull parts and vertebrae	Sánchez-Villagra et al. 2001 ; O'Leary 2004
			Pyrotheria *Proticia venezuelensis*, jaw fragment	Patterson 1977; Sánchez-Villagra et al. 2000
Quiamare Formation	early-middle Miocene	Río Guere site		Vivas and Macsotay 1989
			Boreostemma venezuelensis,	Simpson 1947; Carlini and Zurita, 2010
Chaguaramas Formation	early or middle Miocene	Quebrada Honda site		González de Juana et al. 1980:622-623; Macsotay and Wesselingh 2005

			Astrapotheria *Xenastrapotherium christi*	Stehlin 1928; Kraglievich 1928
Río Yuca Formation/ Parangula Formation	late Miocene-Pliocene age / lower Miocene age	Portuguesa State		Ministerio de Energía y Minas 1997
			'small mammals'	Aguasuelos 1990
			Pseudoprepotherium venezuelanum,	Collins 1934; Hoffstetter 1961
			Sirenid, cranial and postcranial remains	O. Macsotay, pers. comm., In Sánchez-Villagra et al. 2010 ch. 3
Cumaca Formation	Middle Miocene	Tuy Basin, Miranda State		Wesselingh and Macsotay 2006
			Dinomyidae, isolated molar	Horovitz et al. 2010
			Megatheriinae, proximal humerus	Sánchez-Villagra et al. 2010 Ch. 3
La Puerta Formation	Late Miocene	West of Buchivacoa in western Falcón State		Ministerio de Energía y Minas 1997
			Toxodontidae *Gyrinodon quassus*, jaw fragment	Hopwood 1928

Table 1. Late Oligocene-Pliocene fossil mammals from Venezuela exclusive of the Urumaco sequence. Fossils from the Río Yuca and Parángula Formations are listed together because reports from these Formations are of disputed stratigraphical provenance, as summarized by Sánchez-Villagra et al. (2010).

The Urumaco Sequence

Quiroz and Jaramillo (2010) addressed the lithostratigraphy and the sedimentary environments of the Falcón Basin based on new geological and palaeontological data and discussed the paleoenvironmental evolution in relation to the tectonic history of the basin, controlled by the interaction between the Caribbean and South American plates. A sequence of formations in this Basin consists of more than 9000 m of shallow to marginal marine sediments which include not only the Urumaco sequence but also the underlying Agua Clara, Cerro Pelado, and Querales Formations (Johnson et al. 2009) (Fig. 2). Absolute dating of rocks of the Falcón Basin has never been reported, so all age determinations are based on stratigraphical comparisons based on microfossils (Díaz de Gamero and Linares

1989; Hambalek et al. 1994) and on estimates based on very few mammalian taxa represented by fragmentary fossils (Linares 2004a) which, as we will discuss here, are very difficult to correlate with well-dated faunas from more Southern faunas of South America.

Four geological formations in the Urumaco area contain diverse fossil mammals, Socorro Fm, Urumaco Fm, Codore Fm, and San Gregorio Fm. The best studied so far is the Urumaco Formation (Aguilera 2004), of late Miocene age (Díaz de Gamero and Linares 1989; Linares 2004 a).

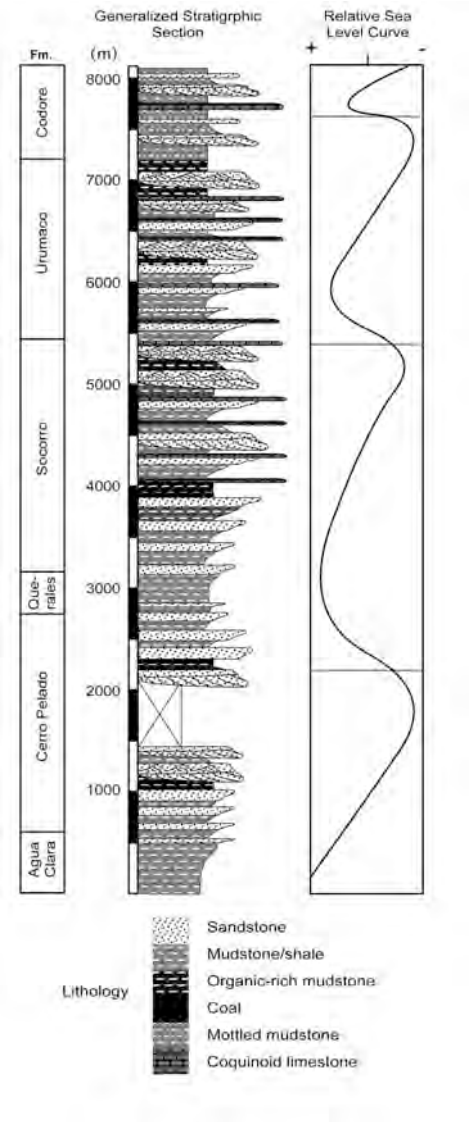

Figure 2. Summary of the Neogene Formations and their main depositional environments in the western Falcón province, Urumaco region. Modified from Quiróz and Jaramillo (2010).

Underlying the Urumaco Formation is the Socorro Formation, of middle Miocene age (Hambalek et al. 1994). The upper part of Socorro Formation is where most fossil vertebrates of this Formation have been found. It preserves mostly deltaic and fluvial deposits (Hambalek et al. 1994). The Socorro Formation outcrops extend for more than 150 km in an east-west direction from Coro to the town of Dabajuro. A thickness of 2209 m was measured in a site 20 km west of Urumaco. The three informal members of the Formation preserve different kinds of deltaic einvironments. Díaz de Gamero and Linares (1989) assigned a middle Miocene age to the Formation on the basis of foraminifera.

The Urumaco Formation is well exposed in the Falcón state coastal plain, along the Urumaco River. Quiroz and Jaramillo (2010) described this formation, informally divided into three members of different thickness (from bottom to top, 615 m, 755 m and 330 m) as consisting of 'a complex intercalation of medium- to fine-grained sandstone, organic-rich mudstone, coal, shale, and thick-bedded coquinoideal limestones with abundant mollusk fragments'. Linares (2004a) assigned a middle to late Miocene age to the Urumaco Formation based on unpublished studies of some terrestrial mammals, but biochronologic correlation of tropical land vertebrates with those of Southern latitudes are unreliable (see Carlini et al, 2006 a, b; Bond et al., 2006). This Formation preserves mostly a deltaic plain.

The wetlands of the Urumaco Formation changed dramatically at the end of the Miocene, and the fluvial systems of the Codore Formation experienced long periods of subaerial exposure and paleosol formation (Quiroz and Jaramillo 2010). The sediments of the fluvial plain of the Codore Formation are dominated by red mudstones. This Formation has a total thickness of 860 m along the Urumaco River, and has been divided into three formal members, Jebe (475 m), Chiguaje (65 m) and Algodones (320 m). The Jebe and Algodones members were deposited in a fluvial setting without marine influence. On the other hand, the

Chiguaje Member represents a transgressive event, and the sandstones and mudstones with associations of oysters and other marine forms such as echinoderms (Mihaljević et al. in review) indicate sedimentation in a low-energy coastal lagoon or bay with reduced salinity. Rey (1990) assigned a late Miocene–early Pliocene age to the Codore Formation, based on planktonic foraminifera in the Chiguaje Member, an age confirmed by Hambalek et al. (1994) based on palynology.

A major phase of inversion took place during the Pliocene, and the conglomeratic facies of the San Gregorio formation represent accumulation in alluvial fans prograding from the south. Its mammalian fauna, currently under study, includes some small rodents, toxodonts, and at least four species of xenarthrans (1 Dasypodidae, 1 Pampatheriidae, 1 Glyptodontidae and 1 Megatheriidae).

The mammals from the Urumaco Sequence

The most recent overview of the mammalian fauna from Urumaco (Table 2) is in the edited book by Sánchez-Villagra et al. (2010). In it, there are contributions on rodents (Horovitz et al. 2010), xenarthrans (Carlini and Zurita 2010), and ungulates (Bond and Gelfo 2010). Fossil sirenians were recently described by Domning and Aguilera (2008). Previous synthetic works on the fauna from this sequence were those of Aguilera (2004) and Sánchez-Villagra and Aguilera (2006); Cozzuol (2006) presented a comparison of the most diverse northern neotropical fossil vertebrate areas including Urumaco. Recent work on mammals from Urumaco until now has been mostly taxonomic (e.g. Bond et al, 2006; Carlini et al, 2006 a, b, c, 2008 a, b; Carlini & Zurita 2010), and in few cases phylogenetic (Horovitz et al. 2006); discussions on the adaptations or paleoecology of these animals have been largely generalized or speculative (Sánchez-Villagra et al. 2003; Aguilera 2004).

TABLE 2

*Marsupialia, Borhyaenidae indet.
Cetacea, Odontocete indet. 1; Odontocete indet. 2
Xenarthra
Megatheriidae *Urumaquia robusta, Proeremotherium eljebe, Proeremotherium n.sp.*
Megalonychidae *Pronothrotherium* sp., and new genus and species
Mylodontoidea *Urumacotherium garciai*, *Mirandabradys socorrensis*, *Mirandabradys urumaquensis, Mirandabradys zabasi*, *Bolivartherium urumaquensis*, *Bolivartherium codorensis*
Glyptodontidae *Boreostemma pliocena, Boreostemma? n.sp.* (fm, San Gregorio)
Pamaptheriidae*, sp.1* (fm Codore)*, sp.2* (fm, San Gregorio)
Dasypodidae*, cf. Propraopus sp.*
Sirenia, Dugongidae *Nanosiren sanchezi*, ?*Metaxytherium*, Sirenia indet.
Litopterna, Protherotheriidae, Megadolodinae *Bounodus enigmaticus*
Notoungulata, *Typotheria Interatheriidae indet.; *Hegetotheria Hegetotheriidae indet.; Toxodontidae indet.
Astrapotheria indet
Rodentia. Caviomorpha, *Phoberomys pattersoni,* cf. *Potamarchus*, *Eumegamys* sp., **Tetrastylus* sp., **Kiyutherium octolaminatus, *Cardiatherium* sp.

Table 2. Mammal faunal list for the Urumaco sequence, including the Socorro, Urumaco, Codore and San Gregorio Formations. Mostly based on a summary by Sánchez-Villagra et al. (2010). Taxa marked by an asterisk were reported by Linares (2004a), but we have not been able to check those reports.

Rodents from the Urumaco Sequence

Remains of rodents are abundant in some localities of the Urumaco Formation, but only three species (*Phoberomys pattersoni,* cf. *Potamarchus, Eumegamys* sp.) have been thoroughly documented and five additional species (*Olenopsis*, *Tetrastylus* sp., *Kiyutherium octolaminatus, Cardiatherium* sp.) have been just reported (Linares 1990, 2004a). These species can be allocated in the Neoepiblemidae, Dinomyidae and Hydrochoeridae (Horovitz et al. 2010). As in all other mammal groups so far sampled from the Urumaco sequence, all forms are of large size (Fig. 3A, B). Absent are groups of caviomorphs represented by species of small size such as spiny rats, abundant in Recent intertropical faunas.

The dinomyid *Eumegamys* Kraglievich 1926 was the first rodent reported from the Urumaco Formation, based on isolated jaw and dental remains (Pascual and Díaz de Gamero 1969). Two isolated molars were assigned to the Potamarchinae cf. *Potamarchus* (Horovitz et al. 2010), from the lower Member of the Urumaco Formation.

The best known rodent from Urumaco is *Phoberomys pattersoni* Mones 1980 (Bondesio and Bocquentin-Villanueva 1988), from which the anatomy of most of the skeleton has been studied in detail (Sánchez-Villagra et al. 2003; Horovitz et al. 2006). The exceptional find for this species is the single one inlcuding associated dental, cranial and postcranial remains. Postcranial anatomy and a combined morphological and molecular parsimony analysis suggested that the pacarana *Dinomys* among living caviomorphs is the closest relative of *Phoberomys pattersoni.*

Several isolated rodent dental and postcranial remains have been recovered from the Urumaco sequence, differing in size and in morphology from those that have been identified as *Phoberomys pattersoni* (Horovitz et al. 2006). There are three

reasons for the difficulties in reaching taxonomic conclusions about these remains, including poor preservation, restricted sampling along a large stratigraphical sequence (Horovitz et al. 2010) and known ontogenetic variation in caviomorphs (Vucetich et al. 2005; Deschamps et al. 2007). Differences in molar size among specimens may represent either different ontogenetic stages or different species. Surely several Neoepiblemidae species are represented in Urumaco, but Horovitz et al. (2006, 2010) have opted for a conservative estimate of species diversity. Given the large size and diversity represented in the Urumaco sequence, future studies could concentrate in the study of growth patterns in the multilaminated and euhypsodont molar teeth of those fossils to elucidate ontogenetic and taxonomic patterns.

Ungulates and Sirenians from the Urumaco Sequence

The materials referred to *Gyrinodon* Hopwood, 1928 by Aguilera (2004) and by Linares (2004a) for the Urumaco Formation was considered by Bond et al. (2006) an indeterminate Toxodontinae (Fig. 3C). The Litopterna proterotheriid Megadolodinae *Bounodus enigmaticus* from Urumaco is well-documented in the taxonomic description by Carlini et al. (2006b). *Bounodus enigmaticus* is represented by a fragmentary maxillar found at the Upper Member of the Urumaco Formation (Carlini et. al. 2006b) (Fig. 3D), and reinforces the hypothesis that the Megadolodinae (*B.* and *Megadolodus*) represent a distinct radiation within the Proterotheriidae on low latitudes (see Carlini et. al. 2006b).

Several native ungulates were reported by Linares (2004a) for the Urumaco Formation. If these were to be confirmed, they would comprise the following taxa, which would signify temporal or geographical expansions (Bond and Gelfo 2010):
- Among the Litopterna, the proterotheriid *Licaphrium* cf. *mesopotamiense* as well as several inderterminate macraucheniid.

- For the Notoungulata, two typotherians, the interatheriid *Protypotherium* sp., the hegetotheriid *Hemihegetotherium* sp., and the toxodontid *Gyrinodon quassus*, and *Ocnerotherium* sp.

- Two indeterminate Astrapotheriidae.

Linares (2004a) also reported the toxodontid *Alitoxodon* sp. for the El Jebe Member of the Codore Formation.

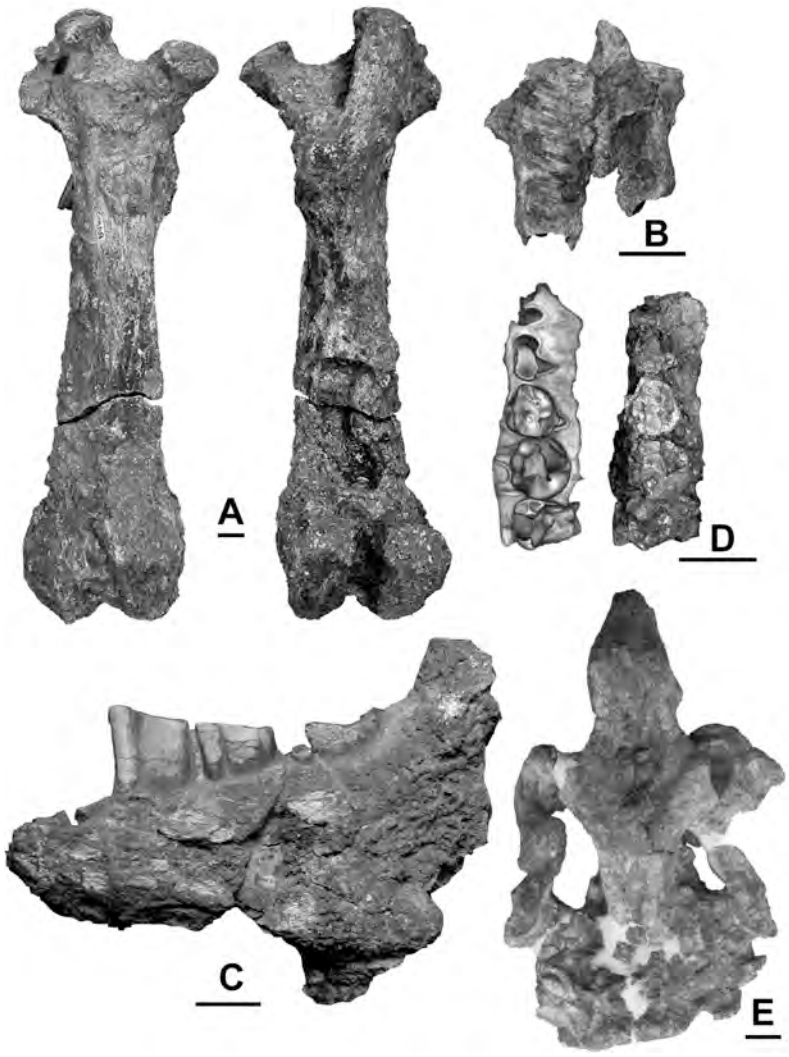

Figure 3. A: Right femur in anterior and posterior views, AMU-CURS-56 of an undetermined rodent from the Urumaco Formation (late Miocene, Venezuela). B: Partial palate with P4-M1 of *Phoberomys pattersonii*. C: Lateral view of a toxodontiid partial left mandible with m1-3 from Urumaco Fm, (UNEFM-CIAAP 616) modified from Bond et al. 2006. D: *Bounodus enigmaticus* (AMU-CURS 44, type), fragment of rigth maxilar in occlusal view, and its drawing, modified from Carlini et al. 2006b. E: Sirenian partial skull in dorsal view, from Urumaco Fm. Scale bar = 2cm.

The Venezuelan Miocene sirenians are represented by four records, the two new species described by Domning & Aguilera (2008) from Urumaco Fm (Fig.3E), several other dugongid vertebrae and ribs from Urumaco (Aguilera, 2004), the possible Miocene trichechids in the Urumaco area (reported by Linares, 1991), and an indeterminate sirenian rib fragments from the early Miocene Cerro La Cruz fauna in adjoining Lara State (Sánchez-Villagra et al., 2004), a fauna similar to that of Urumaco (Domning & Aguilera 2008).

The Tardigrade Diversity of the Venezuelan Neogene

Until recently only two genera of tardigrades were known from the Urumaco sequence, and both were Mylodontoidea from the Urumaco Formation. They are the singular *Urumacotherium garciai* (Boquentin 1984; Negri and Ferigolo 2003) (Fig. 4A), and a second taxon supposed to belong to the otherwise Southern genus *Lestodon* (*L. urumaquensis* and *L. codorensis*, see Linares 2004b) (Fig. 4B). In recent years, Carlini and collaborators (Carlini et al. 2005 a, 2006 a, c, 2008 c) described a very diverse fauna, including clades related with the first emigrants to North America and Caribbean Islands (Carlini et al. 2005a, 2006a, c). This diverse fauna is found in all four Formations of the Urumaco sequence and includes several species of the megalonychid and megatheriid clades (White and MacPhee 2001; Gaudin, 2004).

Most likely due to taphonomical biases, most of the tardigrade taxa from the Urumaco sequence are represented by long bones, most frequently femora and humeri. This was a challenge when we started the study of these fossils, as in order to diagnose the new taxa, a revision of femoral anatomy in other fossil and Recent taxa was necessary. The diversity in the Urumaco sequence is exceptionally large and comparable only to that of the richest sites and times of tardigrade evolution in South America, which include the Late Oligocene of

Patagonia (Deseadan SALMA; see Carlini and Scillato-Yané 2004), early Miocene of Patagonia (Santacruzian) and Late Miocene of the Argentinian Mesopotamian area ("Conglomerado Osífero" of the Ituzaingó Formation; Carlini et al. 2001).

The tardigrade discoveries from Venezuela increase the diversity of megatheriines from northern South America and provide some clues about the differentiation of *Megatherium* and *Eremotherium,* two genera which had their largest diversity in the Pleistocene (Carlini et al., 2006c 2008c).

In the Socorro, Urumaco and Codore Formations, the following number of taxa are recorded: two species of Megatheriinae (Carlini et al., 2006c, b, 2008c), five (undescribed) of other Megatherioidea, and six Mylodontoidea (Carlini et al., 2005a, 2006a). In addition to these taxa, there are at least one Megatheriidae and oneMylodontoidea from the San Gregorio Formation. All the tardigrade taxa within a Formation were not necessarily contemporaneous, as several levels within them are involved. Any case, all the four Formations were deposited on a relatively short lapse of time, and some anagenetic process could be happened (e.g. *Mirandabradis* species, see Carlini et al., 2006a).

All tardigrade species so far found are of large size, with mylodontoids ranging from *Glossotherium* size to animals slighty smaller than *Lestodon trigonidens*. This size distribution is unique among tardigrade assemblages in South America. It is of course possible that a taphonomical bias exists and the tardigrade diversity was thus even larger; we have no records in Urumaco of the small sized tardigrades that are very diverse on the Caribean tardigrade faunas (see MacPhee & White, 2001, MacPhee & Iturralde-Vinent 1994, and bibliography therein).

At least three lineages can be distinguished among the Mylodontoidea of the Urumaco sequence:

1) *Mirandatherium*, a recently described genus (Carlini et al., 2006a) (Fig. 4C) related to *Pseudoprepotherium.* Carlini et al. (2006a) pointed out several important similarities between the skull of *P. confussum* from the Laventan SALMA and *M. socorrensis* from the Socorro Formation. *Mirandatherium* is represented by three species, one from each of the corresponding formations: *M. socorrensis*, *M. urumaquensis* and *M. chihuajensis. Mirandatherium socorrensis* shows some derived features when compared to *Pseudoprepotherium*, such as the proximal and the distal fixation of the fibula over the tibia.

According to Hirschfeld (1985) *Pseudoprepotherium* and *Orophodon* Ameghino from the Oligocene (SALMA Deseadense) of Patagonia are closely related taxa. As a working hypothesis pending future phylogenetic analysis, we follow a taxonomic arrangement in which *Mirandatherium* could be classified as orophodontid (sensu Scillato-Yané 1977a, Carlini & Scillato-Yané 2004, partially in agreement with that of Hoffstetter 1954, 1956, and with McKenna and Bell, 1998; contra Villarroel 2000). After its first occurrence on high latitudes (see Hoffstetter 1954, 1956) in Deseadan (Oligiocene) deposits of Patagonia, where the environment is interpreted as humid subtropical to template (Bellosi, 1995), Orophodontid clade remain restricted to the northern South America. According to Bellosi, a thick shrubby forest covered the area of the San Jorge Basin, while more temperate-cold and humid forest developed at higher elevations near the present Deseado peninsula (and Protopatagonia), especially during the end of the Deseadan (Carlini and Scillato-Yané, 2004). This clade (orophodontids) evolved a large intertropical clade which includes the Octodontobradyinae (Late Miocene – early Pliocene of Brasil) (Santos et al., 1993) and the Orophodontinae (*Pseudoprepotherium* and *Mirandatherium*).

The report of *Glossotheriopsis* in the Socorro Formation by Linares (2004a, fig. 4 A) is based on a partial skull. Carlini et al., (2006a) hypothesized that this skull should be actually allocated to *Mirandatherium socorrensis*, and that it shows

features (as the characteristic cranial shape) more similar to *Pseudoprepotherium* and *Urumacotherium* Compared with the holotype of *Glossotheriopsis pascuali* Scillato-Yané 1978 (see McDonald 1997, fig. 15.3) we see in the specimen shown by Linares (2004a, fig. 4 A) many differences. In *Glossotheriopsis* the rostrum is short and tall, similar to that of *Glossotherium*, whereas it is longer and low in the Venezuelan specimen. Even more significant is the cranial profile (with a unique broken sagital mid-line in lateral view that is absent on southern species were is almost strigt), which is a characteristic of *Mirandatherium socorrensis* from the same Socorro Formation.

2) *Urumacotherium garciai* Bocquentin-Villanueva 1984 (Urumacotheriinae, Negri & Ferigolo, 2003) is highly derived in its dental anatomy, its femoral and tibial shape and the size relations among them (see Carlini et al., 2006a table 1). The molariforms are wide and short, almost laminar in occlusal shape (Fig. 4A).

3) The Lestodontines, represented by *Bolivartherium* (Fig. 4B), which may include "*Lestodon*" sp. (Deschamps et al. 2001), from the Montehermosan of Monte Hermoso, Argentina(Carlini et al., 2006a).

Geographical comparisons and considerations

The Orophodontids, first recorded from the Late Oligocene of Patagonia (Hoffstetter, 1954, 1956), evolved a vast intertropical diversity different from that of the Mylodontidae, which includes the Octodontobradynae (*Octodontobradys*) from the late Miocene - early Pliocene of Brasil (Santos et al. 1993), the Orophodontinae from the late Oligocene to Pliocene (*Pseudoprepotherium* and *Mirandatherium*), the Orophodontinae (*Pseudoprepotherium* y *Mirandatherium*) and the Urumacotheriinae from the late Miocene-Plioceno (*Urumacotherium*).

Urumacotherium has been reported so far outside Venezuela only from the late Miocene - Pliocene of Acre, Brasil (Bocquentin and Guilherme 1999, Negri and Ferigolo 2003). Consequently, the geographical distribution of this clade is restricted to the northern half of South America.

Pseudoprepotherium Hoffstetter is also restricted to the northern half of South America. Besides its presence in the Miocene-Pliocene of Venezuela (Collins 1934, Hoffstetter 1961), it is also reported for the middle Miocene Medio of La Venta, Colombia (Hirschfeld 1985) and for the late Miocene - Pliocene of Acre (Bocquentin and Guilherme 1999).

Orophodon, *Octodontotherium* and *Chubutherium* (Catoi, 1962; ; Scillato-Yané 1977a; Carlini and Scillato-Yané 2004) inhabited Patagonia during the Oligocene, but there are no Orophodontidae in any younger strata in that area. The disappearance of certain groups in the southern-most areas of South America and their persistence in lower latitudes is also exemplified by the Glyptodontidae "Glyptatelinae", present in Patagonia in the Mustersan and the Deseadan. In the Deseadan there were species which reached very large size, such as *Clypeotherium magnum*, with osteoderms of its dorsal shield as thick as 4 cm (Scillato-Yané 1977b). This clade (Glyptatelinae) is present in the Laventan (Middle Miocene) of Colombia (Carlini et al. 1997).

The Megatheriidae

Among the Urumaco Tardigrades, the first Megatheriinae from the Tertiary of Venezuela were described (CARLINI et al. 2006 c), represented by two new genera and species from the Late Miocene - Pliocene. For the Urumaco Formation (Late Miocene) *Urumaquia robusta* CARLINI, BRANDONI & SÁNCHEZ, 2006 was described based on few but significant remains (see CARLINI et al. 2006 c), that have been

collected in the Urumaco outcrops in the 1970's, and posteriorly Carlini et al. (2008c) improve the knowledge of this taxon describing and comparing new remais. For the Codore Fn. (Pliocene) *Proeremotherium eljebe* Carlini, Brandoni & Sánchez, 2006 was described based on an almost complete skull (Fig. 4D), and was originally interpreted close to *Eremotherium*. Regarding the relationships among the species of *Eremotherium*, De Iuliis & Cartelle (1999) stated that *E. eomigrans* and *E. laurillardi* formed a phyletic sequence. No ancestral forms of *Eremotherium* are known so far, but *Proeremotherium eljebe* shows many of the expected characters for an ancestor, something that should be checked in a phylogenetic analysis. Likewise, as *E. eomigrans* and *E. laurillardi* were proposed as forming a phyletic sequence (De Iuliis & Cartelle, 1999), this sequence could have begun in the Pliocene of Venezuela with *Proeremotherium eljebe* (Carlini et al., 2006c). We have new udescribed remains (skull) but from San Gregorio Fn. (Pliocene, but younger than Codore Fn.), that surely belong to a new species of *Proeremotherium* because it shows differences on its basicranial and temporal morphology with *P. eljebe*.

Overviews of the megatheriine remains of the upper Tertiary of South America and their geographic and temporal distribution (CARLINI et al. 2002, 2006 c), show that the Tertiary findings were not frequent at low latitudes. Precisely, the new megatheriines not only extended the knowledge of their diversity in South America, but they led us to speculate about the moment of differentiation of *Megatherium* CUVIER, 1796 and *Eremotherium* SPILLMANN, 1948, both genera with maximum diversity in the Pleistocene. *Urumaquia robusta*, is even larger than the Upper Miocene-Pliocene Argentinean species of *Pyramiodontherium* ROVERETO, 1914 and *Megatheriops* C. AMEGHINO & KRAGLIEVICH, 1921. Some of the morphological features of *U. robusta* (see Carlini et al., 2006c, 2008c) are more derived than those of the taxafrom the Middle Miocene of Argentina. The taxa recorded in the Middle Miocene of La Venta, Colombia, where very likely the smallest and most

gracile Megatheriinae at the time, (see HIRSCHFELD 1985; CARLINI et al. 2006 c) and more plesiomorphic than those of Venezuela.

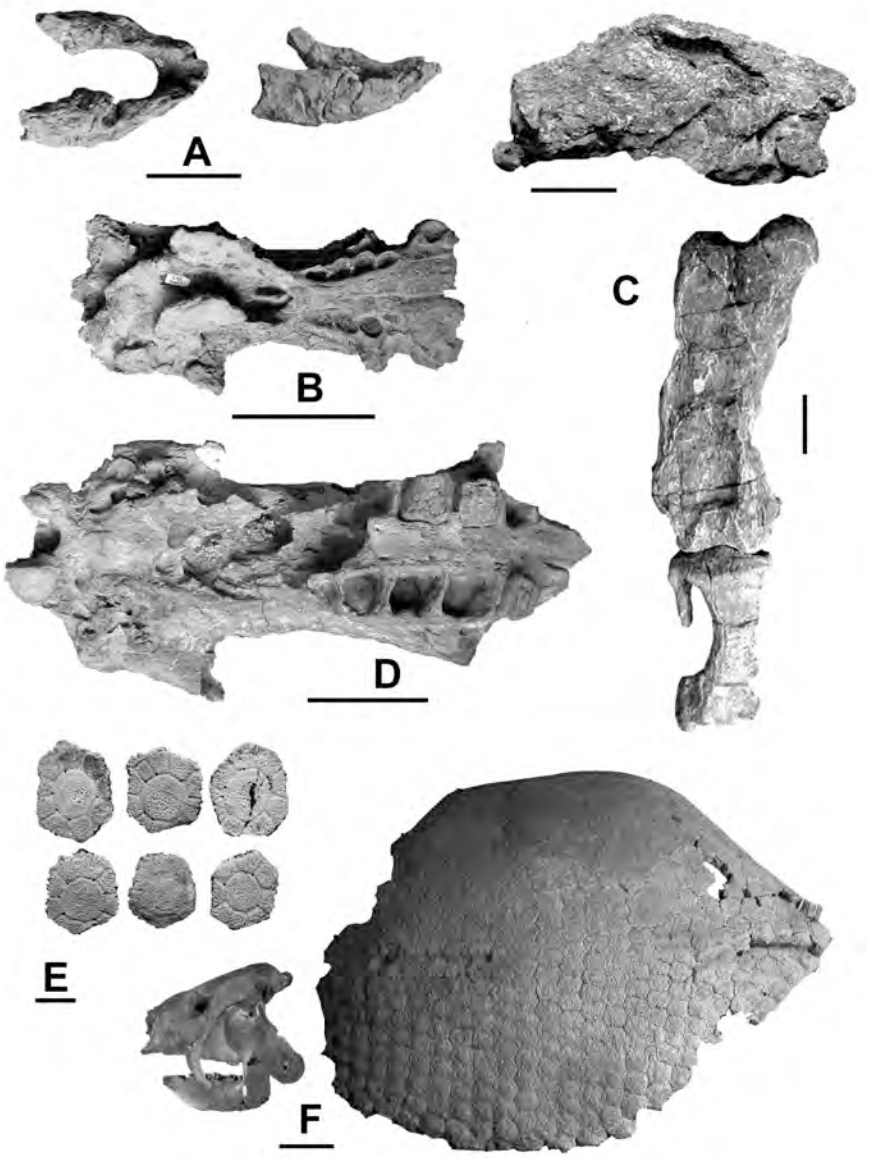

Figure 4. A: *Urumacotherium garciai* (UNEFM-CIAAP 443, type), partial mandible in oclusal and right lateral views, from the Urumaco Formation. B: *Bolivartherium codorensis* (AMU-CURS 130, type) from the Urumaco Formation, partial skull in oclusal view (modified from Carlini et al. 2006a). C: *Mirandatherium socorrensis* (AMU-CURS 29, type) from the Sococrro Formation, crashed skull in right lateral view and, femur and tibio-fibula in anterior view (modified from Carlni et al. 2006a). D: *Proeremotherium eljebe* (AMU-CURS 126, type) from the Codore Formation, partial skull in oclusal view (modified from Carlini et al. 2006c). E: *Boreostemma pliocena* (AMU-CURS 158, type) from the Codore Formation, six dorsal osteodems in external view (modified from Carlini et al. 2008a). F: *Glyptotherium cf. cylindricum* from the uppermost Pleistocene of the Falcón Basin, skull (MCN n/n), mandible (UVC n/n), and dorsal caparace (UNEFM-CIAAP n/n), from different individuals (modified from Carlini et al. 2008b). A, B, C, D, F. Scale bar = 10 cm; E, scale bar = 2cm.

The Cingulata diversity amog the Urumaco sequence

The apparent external resemblance among the four major groups of cingulates (i.e., glyptodonts, pampatheres, armadillos and peltephilids) might suggest close relationships among them, but the paleontological evidence indicates that they have had separate evolutionary histories at least since the Eocene (Scillato-Yané 1986; Flynn and Swisher 1995; Carlini et al. 2005b, in press), that is, for at least 50 million years. In the Venezuelan deposits only glyptodonts, pampatheres and armadillos are kown.

Tertiary Glyptodonts have been known from Venezuela since Simpson´s work (1947), in which he described *Asterostemma venezolensis*, but this remains comes from outside the Urumaco region (Middle Miocene, Santa Inés Fn.) . After that, in 2008 Carlini et al. (2008a) described a new genus *Boreostemma* and trasferred to it all the *Astreostemma* species described for low latitudes (see also Carlini and Zurita., 2010); this new genus was placed into Glyptodontinae glyptodonts and not as a Propalaehoplophorinae (as *Asterostema* is). Previously, the Glyptodontide Glyptodontinae had its oldest known records from sediments assignable to the late Miocene-Pliocene of northwestern Argentina (*Glyptodontidium tuberifer*). However, the recent discoveries in northernmost South America (Colombia and Venezuela), older than the Argentine fossils, suggest that the glyptodontines could have originally arisen at those lower latitudes, and are exemplified by *Boreostemma* (Carlini et al. 2008a) from the Codore Fn (Pliocene) (Fig. 4E). During the lapse of time, that Pascual and Bondesio (1982) have designated as “Age of the Southern Plains” because of the great development of open extensions that were quite probably occupied by grasslands (between 11 and 3 million years ago), the glyptodontines could have migrated southwards. No glyptodontids are known from Socorro Fn., but there are very few osteoderms undescribed in the Urumaco Fn., that could be related with

the Codore´s ones. Recently, in the San Gregorio Fn. (Pliocene) we found some osteoderms that represent a taxon close to *Boreostemma codorensis* (but different); these remain are under study all toghether with the other xenarthrans founded from the same locallity.

From a biogeographical perspective, the glyptodontines (along with the glyptatelines) seem to be the only glyptodonts that were capable of migrating to more northern latitudes during the “Great American Biotic Interchange” (GABI), reaching North America about 2.7 million years ago, may be early (for further dicussion see Carlini and Zurita 2010).

After that, and during the latest Pliocene and the Pleistocene, the glyptodontines were the more common glyptodont forms, with a remarkable latitudinal distribution in South America that ranged from southern Argentina to Venezuela. Until recently, all the species occurring in this subcontinent were included in a single genus: *Glyptodon* Owen, but in a recent paper Carlini et al. (2008b) proposed that the glyptodontines from the upper most Pleistocene of Venezuela belongs to the North American genus *Glyptotherium* that reentered South America (Fig. 4F) (as apparently happended too with *Pachyarmatherium*, see Carlini and Zurita, 2010; Rincón et al., 2008).

The pampatheriids

Although the pampatheriids did not reach the diversity of glyptodonts or dasypodids during their evolutionary history they were capable of moving across Central America in the Pliocene during the Great American Biotic Interchange (Stehli and Webb 1985; Morgan, 2005; Morgan and Hulbert 1995; Scillato-Yané et al. 2005). The earliest uncontested record of a pampathere corresponds to

Scirrotherium, from the middle Miocene of La Venta, Colombia. On the Urumaco sequence, we have pampatheriids in Urumaco, Codore and San Gregorio Fns.; except those of the Codore Fm, were there are a number of associated osteoderms belongin fron the same specimen, those of Urumaco and San Gregorio Fns. are actually scarse. Notwithstanding, they allow us to speculate that the San Gregorio species is morphologically close to oldest *Holmesina* species (*H. floridanus*) from the Blancan (Pliocene) of North America, but smaller.

The Dasypodidae

In Venezuela, there are no reccords of Tertiary dasypodids, except for the few remains of Dasypodinae that were founded recently at the San Gregorio Formation (Pliocene). They may be related to the genus *Propraopus*, a genus which recently Rincón et al. (2008) synonymized with *Dasypus*, but we preferr to keep it as valid until further analisys are conducted. Apparently, the fauna of this formation could be the closest temporally to the first continuous connections (late Pliocene) between South and North America.

Summary and Conclusions

The fossil record of northern latitudes of South America is particularly poor. In contrast, faunas from Patagonia and Central Argentina have been intensively studied for decades and provide the framework upon which our understanding of evolution in the continent is based (Pascual et al. 1996; Flynn and Wyss 1998).

The study of the few intertropical fossil faunas known such as those of Acre (Miocene, Brazil) and La Venta (middle Miocene, Colombia) show that the faunas from northern South America displayed significant differences from coeval

Patagonian ones. This pattern is further emphasized with the recent discoveries of tardigrades from Venezuela.

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12

AN INTRODUCTION TO CINGULATE EVOLUTION AND THEIR EVOLUTIONARY HISTORY DURING THE GREAT AMERICAN BIOTIC INTERCHANGE: BIOGEOGRAPHICAL CLUES FROM VENEZUELA

Alfredo A. Carlini and Alfredo E. Zurita

The Xenarthrans: An Overview

The Xenarthra are a peculiar group of mammals, with a long and successful evolutionary history that took place in America during most of the Cenozoic, from the Early Paleocene to the present (Scillato-Yané 1986; Carlini et al. 2005; Hill 2006). Their current diversity (about 13 genera with some 31 species) does not reflect the remarkable diversity that they reached in the past, with more than 160 genera (see McKenna and Bell 1997; Hoffstetter 1958; Paula Couto 1979) that probably included more than 400 species. The origin of this clade was quite probably in America, although fossil forms have also been found in Eocene sediments of Antarctica, from the time when the latter continent was connected to southern South America, during the Early Cenozoic (Carlini et al. 1990; Vizcaíno and Scillato-Yané 1995). In addition, in 1981 *Eurotamandua* was described for the European Eocene as a Vermilingua (Storch 1981), although the affinities of this species are a matter of controversy (Szalay and Schrenck 1998; Rose et al. 2005), and today it is not considered as a xenarthran.

The living Xenarthra includes sloths, anteaters, and armadillos. This clade has played a special role in the discussions about the common ancestor of placental mammals, given that xenarthrans are frequently interpreted as a basal group in the radiation of placentals. According to some estimates made on the basis of molecular clocks, the divergence of xenarthrans from other placentals could have taken place during the Early Cretaceous (Springer and Murphy 2007). However, the paleontological evidence does not support this estimate (Asher et al. 2005; Wible et al. 2007).

The name of the group, "xenarthra," derives from the possession of a series of accessory vertebral apophyses (xenarthral apophyses) characteristic of these animals (Gaudin 1999). They are also characterized by teeth that are very similar to each other, have a relatively simple morphology, and lack enamel (Grassé 1955; Hoffstetter 1958; Paula Couto

> [S]cientists should resist the temptations of scientism. They should always remember, as I think Darwin always did, that science is tentative and fallible. Science does not solve all the riddles of the universe, nor does it promise ever to solve them. Nevertheless it can sometimes throw some unexpected light even on our deepest and probably insoluble riddles.
>
> K. R. Popper, *Natural Selection and the Emergence of Mind*

1979; Hill 2006). The term "edentates" (which has also been used to designate the xenarthrans) is thus incorrect, because the only truly toothless xenarthrans are the anteaters (Vermilingua), in which this character is unquestionably associated with their exclusively myrmecophagous diet.

A first major division within the Xenarthra distinguishes two clades. Those forms with a fur cover are the Pilosa (pilosans), comprising the Tardigrada, commonly known as sloths, and the Vermilingua, the anteaters. The second major group is the Cingulata (cingulates), characterized by having their body covered by an "armor" shell formed by articulated and joined osteoderms, analogous to the dermal bones present in some reptiles (Engelmann 1985; Gaudin and Wible 2006). These osteoderms form the dorsal carapace that covers most of the body; the head is protected by a cephalic shield, and the tail is encased in a caudal shield. Four well-characterized groups are included in the Cingulates: the Dasypodidae (armadillos), the Pampatheriidae (pampatheriids), the Glyptodontidae (glyptodonts) and the Peltephilidae (peltephilids). A fifth clade, the Palaeopeltidae (paleopeltids), is difficult to diagnose due to the lack of significant records and morphological features.

The Cingulates: Origin and Evolution

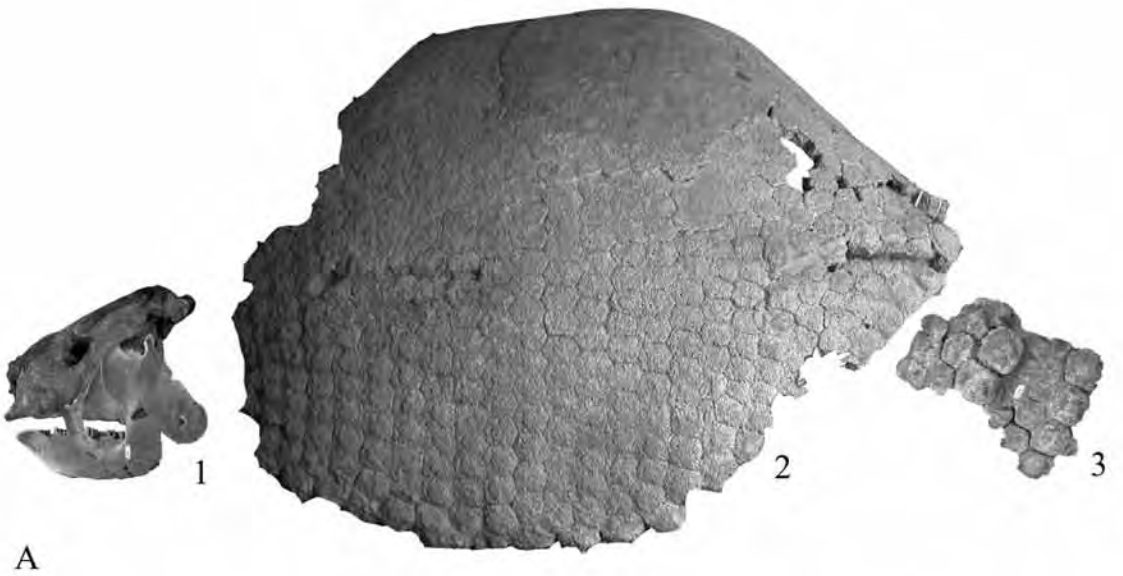
The earliest records of xenarthrans correspond to cingulates, more specifically, to a species of Dasypodidae, *Riostegotherium yanei*, from the upper Paleocene of Brazil (see Bergqvist, Abrantes, and Avilla 2004). Later, during the Eocene (Casamayoran Age), the cingulates underwent significant radiation (Carlini et al. 2002a, b, c, 2004); this was probably the time of differentiation of the Glyptodontidae, including the poorly known Glyptatelinae (Ameghino 1902; Scillato-Yané 1986; Carlini et al. 2005).

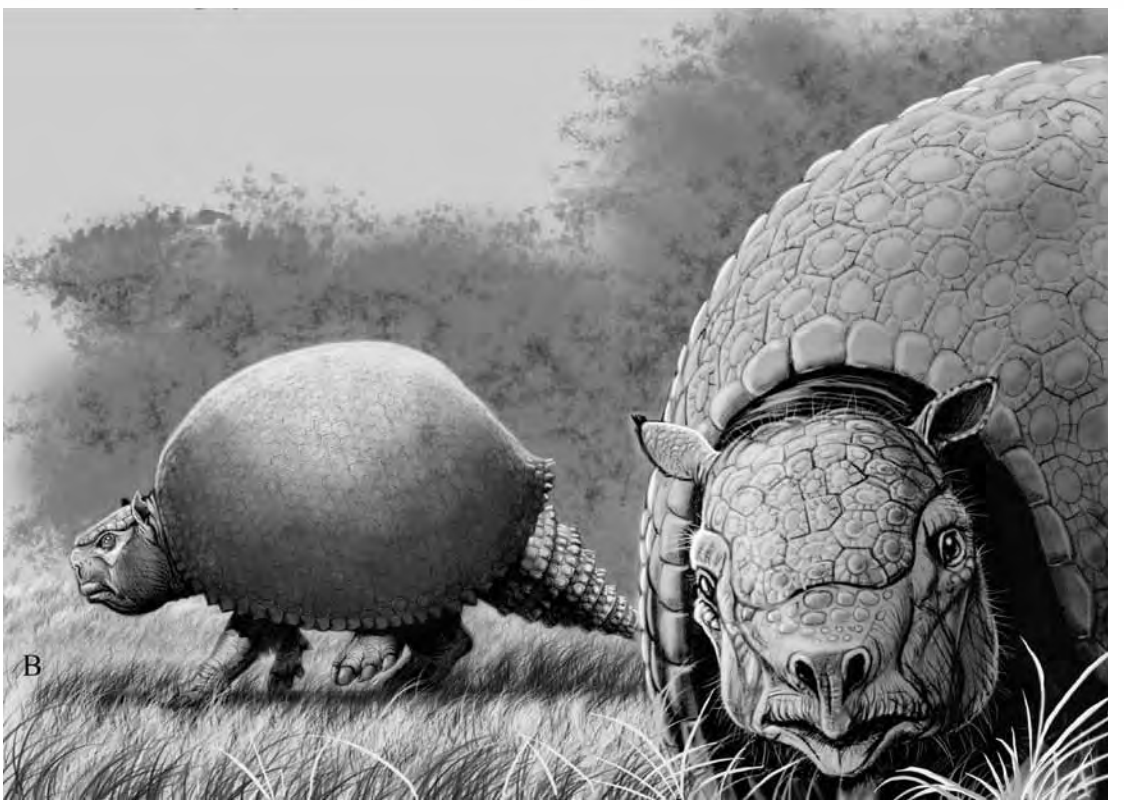
Although the apparent external resemblance among the four major groups of cingulates (i.e., glyptodonts, pampatheres, armadillos, and peltephilids) might suggest close relationships among them, the paleontological evidence clearly indicates that these four major groups have had separate evolutionary histories at least since the Eocene (Scillato-Yané 1986; Flynn and Swisher 1995; Carlini et al. 2005), that is, for at least 50 million years.

Fig. 12.1. *opposite* *Glyptotherium* cf. *cylindricum.* A1: skull (MCN n/n) in lateral view. A2 (CIAAP n/n): articulated osteoderms of a partial carapace in left lateral view. A3 (UNEFM 1540): articulated osteoderms of two partial caudal rings, each of them formed by three osteoderm rows. Scale bar = 10 cm. B: depiction of *Glyptotherium* cf. *cylindricum. Artwork by Jorge González.*

The Glyptodonts

Three basic features define glyptodonts. They possess an undivided dorsal carapace, in contrast with those of armadillos, peltephilids, and pampatheriids. Partially mobile bands may be present on the sides of the body, in both basal (Glyptatelinae and Propalaehoplophorinae) and derived forms (e.g., *Panochthus*). Glyptodonts have one of the highest hypsodonty indices of all terrestrial animals (Gillette and Ray 1981), and the particular





trilobed form of the molariform teeth, particularly the posteriormost ones, formed by three aligned proximodistally compressed prisms, is unique. Finally, the skull of glyptodonts is short and very high, and the dental series may be greatly extended posteriorly.

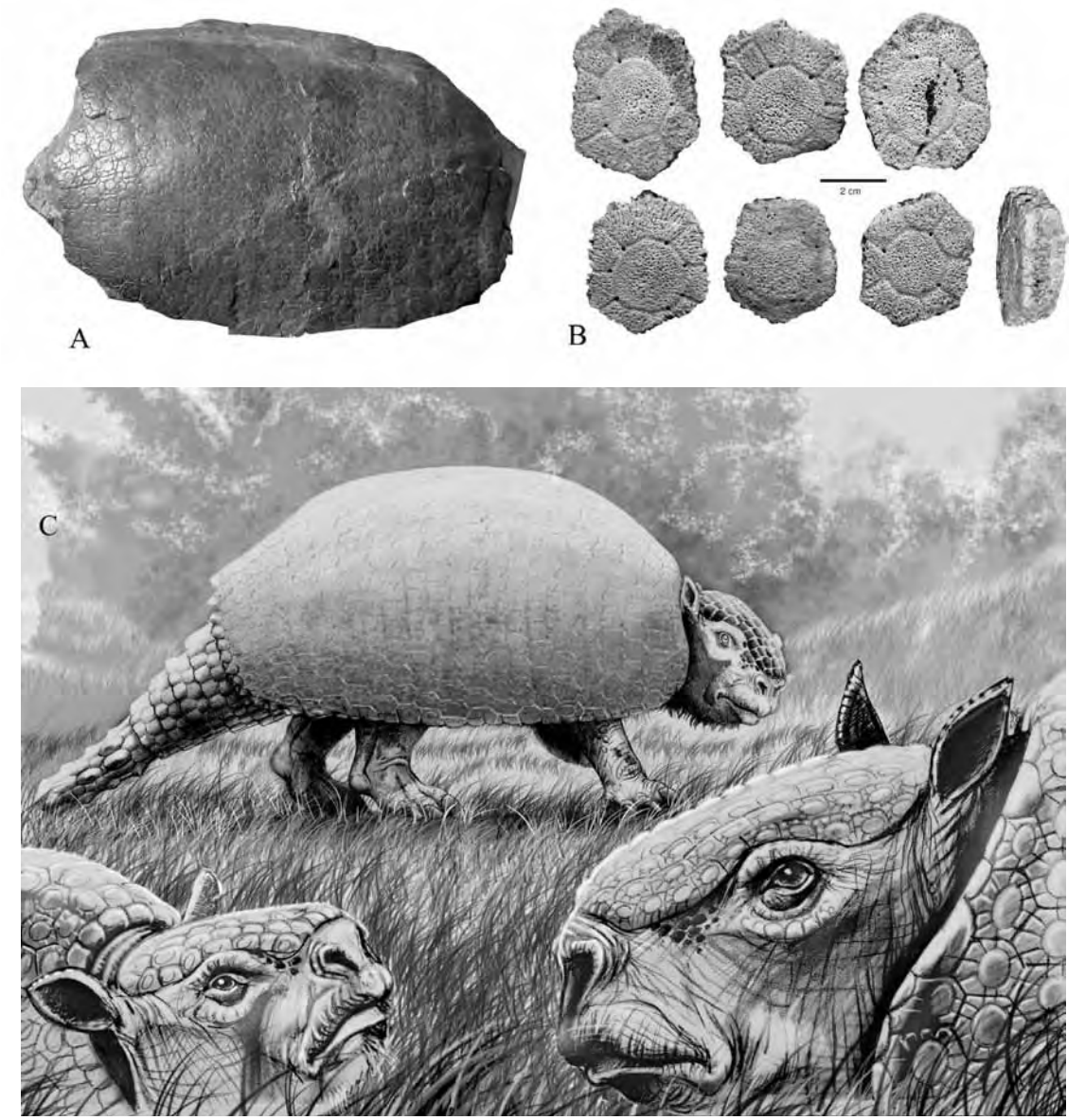
Glyptodonts were herbivorous grazers, adapted to open grassy and shrubby environments. In the Oligocene and Pleistocene they reached

gigantic sizes, including forms more than 3 m long and masses of up to two tons (Scillato-Yané 1977; Scillato-Yané and Carlini 1998; Fariña and Vizcaíno 1999). Some of them (for instance, the genus *Doedicurus*) had a mace-like structure armed with horny spikes at the tip of the caudal sheath, a structure evidently used for defensive purposes. Such structures could also have been used during intraspecific combats, because some specimens have been found with their armor showing fractures that correspond in shape to these tail-maces (Lydekker 1894).

The long evolutionary history of glyptodonts is mostly restricted to South America, although they were also part of the contingent that migrated toward North America at least 2.7 Ma, after the definitive establishment of the Panamanian isthmus (Gillette and Ray 1981; Webb 2006; Carlini, Zurita, and Aguilera 2008a) (fig. 12.1). The first unquestionable records of glyptodonts date back to the Late Eocene (35 Ma) of Argentinean Patagonia, and correspond to the species *Glyptatelus fractus*, originally recognized and described in 1902 by Florentino Ameghino. The subsequent history of the glyptodonts was long and successful, as reflected by about sixty-five recognized genera (see McKenna and Bell 1997). Their last records are after the Pleistocene–Holocene boundary, close to 10 ka, when a massive extinction event caused the disappearance of the majority of the large mammals and all the megamammals (Cione, Tonni, and Soibelzon 2003).

Among the greatly diverse glyptodonts, the Glyptodontinae (glyptodontines) includes some of the most conspicuous forms (fig. 12.1). These are recognizable (and differentiable from other groups) by the conical, tubercle-shaped osteoderms that form the carapace margins. In addition, the ornamentation of their dorsal carapace osteoderms is quite characteristic: each osteoderm has a five- or six-sided central figure encircled by a row of smaller peripheral figures. Deep, wide sulci with parallel margins separate the central figure from the peripherals, and the latter from each other (Ameghino 1889; Pascual, Ortiz-Jaureguizar, and Prado 1966; Carlini et al. 2008b). In addition, all their teeth are molariform and present secondary ramifications of the hard central dentine, a feature exclusive to these glyptodonts.

Until recently, the oldest known records of the Glyptodontinae came from sediments assignable to the Late Miocene–Pliocene of northwestern Argentina (*Glyptodontidium tuberifer*); however, recent discoveries in northernmost South America (Colombia and Venezuela), older than the Argentine fossils, suggest that the glyptodontines could have originally arisen at those lower latitudes. This is exemplified by *Boreostemma* (fig. 12.2), described by Carlini et al. (2008b). Later, during the interval that Pascual and Bondesio (1982) have designated as "Age of the Southern Plains" because of the great development of open extensions that were quite probably occupied by grasslands (between 11 and 3 Ma), the glyptodontines could have migrated southward following certain "biogeographical routes."



From a biogeographical perspective, the glyptodontines (along with the glyptatelines) seem to be the only glyptodonts that were capable of migrating to more northern latitudes during the Great American Biotic Interchange (GABI), reaching North America about 2.7 Ma. However, new remains of glyptodontines have recently been described in north-central Mexico, from sediments dated at about 3.9 Ma (Carranza-Castañeda and Miller 2004). If this record is confirmed, it poses several questions about the chronology of GABI. As mentioned above, a different glyptodont lineage (the Glyptatelinae) could have eventually migrated to North America, but the present evidences are contradictory, because some researchers consider that the species found in southern Florida

Fig. 12.2. A: *Boreostemma venezolensis,* partial carapace in lateral view. B: *Boreostemma pliocena* Carlini et al. 2008, plates corresponding to the dorsal or posterodorsal region of the carapace (six in external view, one in lateral view). C: Restoration of *Boreostemma pliocena. Artwork by Jorge González.*

(USA) corresponds to an armadillo rather than a glyptodont (Downing and White 1995; Rincón, White, and McDonald 2008).

During the latest Pliocene and the Pleistocene, the glyptodontines were among the dominant glyptodont forms, with a remarkable latitudinal distribution in South America that ranged from southern Argentina to Venezuela. Until recently, all the species occurring in this subcontinent (about thirteen, although the validity of many is questionable) were included in a single genus: *Glyptodon* Owen. These glyptodonts are morphologically characterized by their large size, with a mass of up to two tons. Their anatomical features are an interesting combination of highly specialized characters with the remarkable persistence of some features considered primitive for glyptodonts, such as the possession of caudal rings and five digits in the feet.

The Pampatheriids

The Pampatheriidae were traditionally included as the Pampatheriinae within the Dasypodidae, due to the external resemblance between both groups. Later on, Patterson and Pascual (1968) removed the pampatheriids from the dasypodids, and the current consensus is that they are indeed a distinct lineage of cingulates (Scillato-Yané, 1986; De Iuliis, Bargo, and Vizcaíno 2000). However, the phylogenetic relationships of pampatheriids to the other two major cingulate groups (Glyptodontidae and Dasypodidae) are still poorly known. Some authors (e.g., Hoffstetter 1958; Cartelle and Bohórquez 1985) hypothesized that they are closely related to the dasypodids, whereas others (e.g., Carlini and Scillato-Yané 1993; Engelmann 1985) supported a closer relationship to the glyptodonts.

Morphologically, the pampatheriids differ from the dasypodids by their larger size and by having the pelvic and pectoral shields separated by only three transverse mobile bands. In addition, each dorsal carapace osteoderm has an external surface covered by small perforations, with a low central area in which there is a slightly central figure. Proximally, over the anterior border, the osteoderms present a variable number of larger perforations, which can continue over the lateral borders; in some genera, there is a marked peripheral zone that is more rugose. Pampatheriids also have bilobed molariforms (Edmund 1987, 1996; Scillato-Yané et al. 2005; Gaudin and Wible 2006) (fig. 12.3).

Although the pampatheriids did not reach the diversity of glyptodonts or dasypodids during their evolutionary history, they were capable of moving across Central America in the Pliocene, during the Great American Biotic Interchange (Stehli and Webb 1985; Morgan and Hulbert 1995; Scillato-Yané et al. 2005). The earliest uncontested record of a pampathere corresponds to *Scirrotherium*, from the Middle Miocene of La Venta, Colombia. Among their more recent records, three genera have been recognized for the Late Miocene–Pliocene (*Kraglievichia*, *Vasallia*, and *Plaina*) (see Castellanos 1927, 1937) and two for the Pleistocene

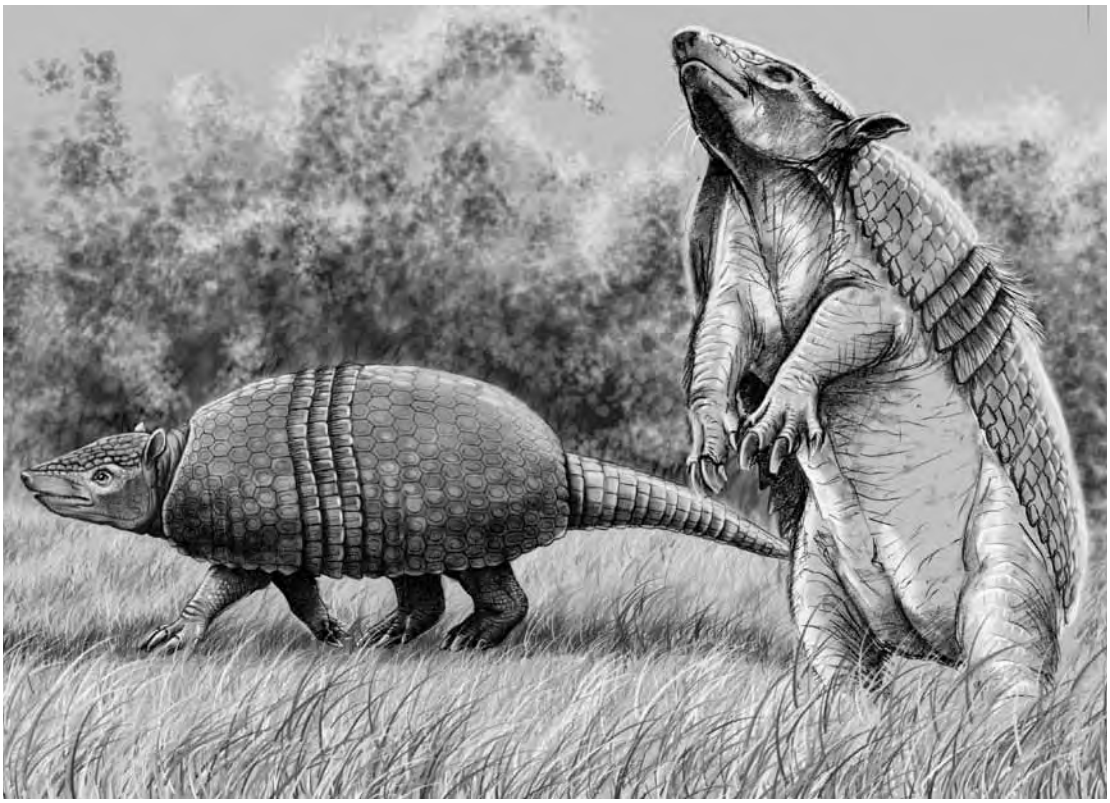


Fig. 12.3. Restoration of a pampatherid from the Pliocene of Venezuela. *Artwork by Jorge González.*

(*Holmesina*, *Pampatherium*). The latter had ample latitudinal distribution, given that their records range from southern Buenos Aires province (Argentina) to the United States (Edmund 1996; Scillato-Yané et al. 2005).

Like the glyptodonts, the pampatheres have been interpreted as basically herbivorous forms (Winge 1941). More specifically, craniomandibular and dental studies suggest that *Pampatherium* was adapted to consumption of more abrasive plant matter (characteristic of arid cold climates) compared to *Holmesina*, which was adapted to warmer, more humid climates (De Iuliis, Bargo, and Vizcaíno 2000; Scillato-Yané et al. 2005).

The Dasypodidae

As already mentioned, the Xenarthra with the longest temporal record are the Dasypodidae, with their oldest records from the Early to Middle Paleocene (Itaboraian) of Brazil (Scillato-Yané 1976; Bergqvist, Abrantes, and Avilla 2004). The diversity of this group is the highest among the Cingulata. The Dasypodidae are characterized by a cover of osteoderms separated into a cephalic shield, a dorsal carapace (including a scapular portion as well as mobile bands and a pelvic portion), and a caudal shield (Hoffstetter 1958; Paula Couto 1979). In contrast to glyptodonts and pamapatheres, dasypodids have a wide range of feeding habits, as observed

in living species and inferred on the basis of craniodental features. The diets are largely omnivorous and opportunistic, and across species include insectivory, faunivory, occasional necrophagy, and even specialized herbivory (Redford and Eisenberg 1992). This dietary variety is associated with a large taxonomic diversity in the group. The earliest representatives of the two main groups (Carlini et al. 2005), the dasypodines and the eupharctines, can first be clearly identified in the Eocene (ca. 42 Ma). The dasypodines are well represented in warmer and more humid environments than those associated with euphractines. The divergence of these two groups took place around a time of major climatic change in the southern cone of the continent (Carlini, Ciancio, and Scillato-Yané 2004, 2005). Among the Dasypodidae, only the dasypodines participated in the GABI, being recorded in North America since the Late Pliocene (ca. 2.4 Ma; Bell et al. 2004; Webb 2006). According to Webb (2006) and Morgan (2005), the Dasypodinae found in older deposits are *Dasypus* (*D. bellus*), exhumed from sediments of about 2.2–2.7 Ma, with a biochron extending until the Late Pleistocene (Rancholabrean). On the other hand, *D. novemcinctus* has its first records in North America in recent times, and still is part of the North American fauna (Woodburne, Cione, and Tonni 2006).

In Venezuela, a few remains of the Dasypodidae Dasypodinae are known, in the San Gregorio Formation (Pliocene), and may be related to the genus *Propraopus* (a genus that recently Rincón, White, and McDonald 2008 synonymized with *Dasypus*) (fig. 12.4). Apparently, the fauna of this formation could be the closest temporally to the first continuous connections (Late Pliocene) between South and North America.

The Great American Biotic Interchange (GABI) and Its Chronological, Geological, and Biogeographical Context

The faunal interchange between South and North America that took place during the Plio-Pleistocene as a consequence of the definitive establishment of the Panamanian bridge is one of the most critical biogeographical events in the recent Cenozoic history of America (see Webb 1985, 2006; Pascual and Webb 1989; Pascual and Ortiz-Jaureguizar 1990; Tonni et al. 1992; Pascual, Ortiz-Jaureguizar, and Prado 1996; Carranza-Castañeda and Miller 2004; Woodburne, Cione, and Tonni 2006, among others).

This connection between North and South America was a gradual process, extremely complex from a geological perspective. The rise and consolidation of this continuous corridor was strongly influenced by the Pliocene Diaguita phase, which brought about the definitive biogeographical connection between both subcontinents (Pascual, Ortiz-Jaureguizar, and Prado 1996). In the first stages (between 9 and 3 Ma), an island chain was established. Later, during the Late Pliocene, a continuous land connection was formed (Webb 2006). The recent discovery of South American immigrants (glyptodonts, sloths, and capybaras) in central Mexico, in sediments dated between 4.7 and 3.6 Ma, strongly

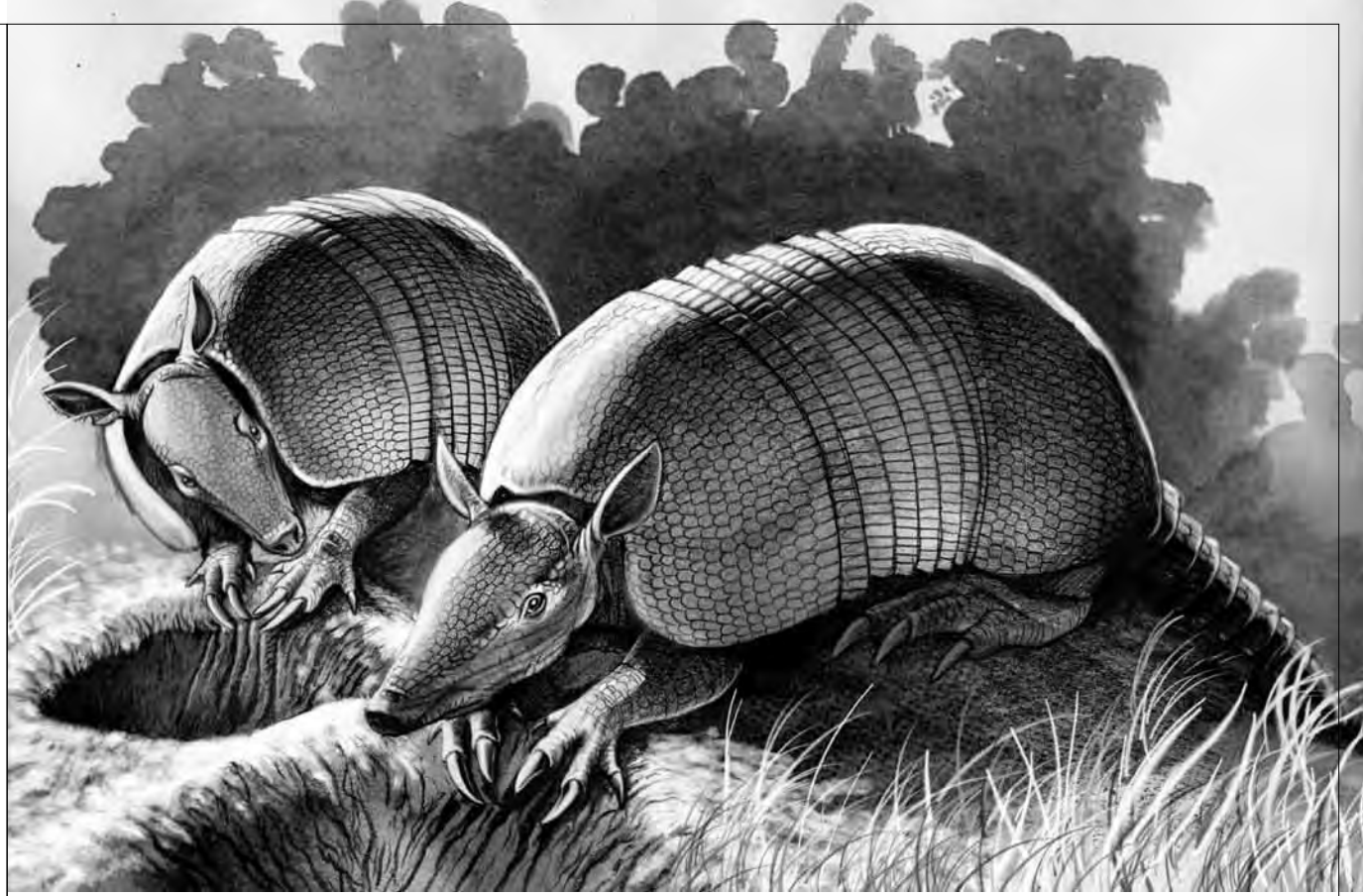


Fig. 12.4. Restoration of cf. *Propraopus* from the late Pliocene of Venezuela. *Artwork by Jorge González.*

suggests that a continuous land connection could have existed (at least temporarily) more than a million years before what has been traditionally hypothesized (Carranza-Castañeda and Miller, 2004; Flynn et al. 2005).

Undoubtedly, the great latitudinal expansion of large open grassland areas during the Pliocene and Pleistocene glacial periods must have been a major factor to stimulate and facilitate migratory processes (Clapperton 1993; Cione, Tonni, and Soibelzon 2003; Rabassa, Coronato, and Salemme 2005), through biogeographical corridors that probably ranged from northern South America (Venezuela) to the south of the current Pampean region in Argentina (Ortiz-Jaureguizar and Cladera 2006).

This notable event had a profound impact on the composition and later evolution of vertebrate communities in South America. Some mammalian orders (for example, most of the large carnivores, the artiodactyls, perissodactyls, and proboscideans) made their first appearance in a continent that had previously existed as an island-continent during most of the Cenozoic and that harbored a very particular fauna that included endemic orders such as the Litopterna, Notoungulata, and Xenarthra. Some authors (Webb 2006) have calculated that approximately thirty-five families of mammals and one of birds were involved in the GABI. An interesting aspect of the latter event was its remarkable asymmetry: the Holarctic emigrants included about forty-five genera, whereas the southern forms that invaded North America were restricted to approximately thirteen genera (Woodburne, Cione, and Tonni 2006).

Nevertheless, South America was not completely isolated during the Cenozoic: for instance, the primates (*Branisella boliviana*) and some rodent groups entered this continent about 30 Ma, arriving with high probability from the western coast of Africa by way of natural rafts; other groups, such as the tardigrade xenarthrans, were able to cross to North America (California and Florida) about 8 Ma (*Pliometanastes*), probably by swimming between islands (Webb 2006). The recent discovery of a semi-aquatic sloth in Pliocene sediments from Peru (De Muizon and McDonald 1995) reinforces this hypothesis. Likewise, the presence of a proboscidean (*Amahuacatherium*) from about 9 Ma has also been recorded in Peru (Campbell, Frailey, and Pittman 2000), although this age assignment is not accepted by all researchers. As in the previous case, the fact that current elephants are able to swim for distances of over thirty miles allows the possibility that these putative first proboscideans could have been able to cross the island chain in Central America.

In South America, the first stages of the GABI are evidenced by the entry of some groups of small carnivores, such as the procyonids (*Cyonasua*), with records dating from 7 to 7.5 Ma (Woodburne, Cione, and Tonni 2006). The arrival of these first immigrants chronologically (and suggestively) coincides with what was possibly the maximum latitudinal expansion of the southern plains ("Age of Southern Plains"; see Pascual and Bondesio 1982), so named by reason of the latitudinal range that these plains would have attained between 11 and 3 Ma (Ortiz-Jaureguizar and Cladera 2006).

Nevertheless, it currently seems evident that the entry of the taxa of Holarctic origin into South America was a more gradual process than has traditionally been conceived. This is shown by the fact that the relative abundance and diversity of the immigrant taxa is very low in the 3.9–1.8 Ma interval (Chapadmalalan and Marplatan Ages) (Tonni et al. 1992; Cione and Tonni 2001), but increases from the earliest Pleistocene, about 1.7 Ma (Cione and Tonni 1995a,b, 2005).

In fact, a long-standing hypothesis proposes that the entry of immigrants was one of the fundamental factors behind the extinction of several endemic South American lineages, whether through competition to exploit the same ecological niches (Simpson 1950, 1980), or because of the introduction of pathogens against which the endemic fauna had no immunological defense (due to their long isolation) (Ferigolo 1999).

As we have stated above, the chronology of this migratory event has been recently contested by the finding of glyptodontines in Mexico, in sediments dated at about 3.9 million years. However, specialists have reached some consensus to temporally locate the beginning of GABI at around 2.7 Ma. Evidence for this is mainly provided by the first known records of South American lineages in the southern United States.

Consequently, the history of the migrations of cingulate xenarthrans (in particular, the glyptodonts and pampatheriids) has been reinterpreted within this biogeographical and temporal framework.

According to the traditional scheme, the GABI has been interpreted (see Matthew, 1915; Simpson, 1980; Webb, 1976, 1978) by most authors as a unidirectional process, in which the North American forms arrived in South America and the southern taxa reached North America. However, it has been shown that the processes involved are usually much more complex (Gould 2002).

Within this theoretical framework, the cingulate xenarthrans have always been supposed to agree with this simplified unidirectional migratory pattern. Three of the four major clades of Cingulata participated in the GABI: glyptodonts, dasypodids, and pampatheriids.

The Glyptodonts during GABI

Present evidence indicates that two glyptodont clades probably participated in the GABI, namely the glyptodontines and the glyptatelines (Gillette and Ray 1981; Morgan and White 2005). As previously mentioned, the Glyptatelines are the glyptodonts with oldest records, and their phylogenetic and biogeographical history is still unclear (Hoffstetter 1958; Vizcaíno, Rinderknetcht, and Czerwonogora 2003). The main diagnostic feature in their dorsal carapace osteoderms is the ornamentation, consisting of a central figure that reaches the posterior margin, surrounded by few peripheral figures. These forms have been found in the Oligocene of Argentine Patagonia and in Bolivia, and later in the Middle Miocene of La Venta, Colombia (ca. 13 Ma; Carlini et al. 1997) and in the Late Miocene of Uruguay (Vizcaíno, Rinderknetcht, and Czerwonogora 2003). Concerning their record, there exists a particularly problematic Cingulata, *Pachyarmatherium leiseyi* from the Late Pliocene–Early Pleistocene (2.4 Ma) of the state of Florida, USA. It was originally recognized by Downing and White (1995) as a dasypodoid; however, it is currently classified as a Glyptodontidae Glyptatelinae (see McKenna and Bell 1997). Were the latter to be confirmed, it would represent a remarkable latitudinal and temporal extension for the Glyptatelinae. In addition, it would demonstrate that the Glyptodontinae were not the only Glyptodontidae THat migrated to North America during the GABI.

The history of the other group of glyptodonts (the glyptodontines) is better known than that of glyptatelines, although it has been partially reinterpreted in recent works by Carlini, Zurita, and Aguilera (2008a) and Carlini et al. (b). Until recently, the oldest records of glyptodontid Glyptodontinae (*Glyptodontidium tuberifer*) were restricted to the Late Miocene–Pliocene (7–3.5 Ma) of southernmost South America (Cabrera 1944). Based on this, the group was assumed to have differentiated in southern areas, and probably from another glyptodont clade, the Propalaehoplophorinae from Argentine Patagonia (Scott 1903–1904), which had also been reported for the Miocene of Colombia and Venezuela, in sediments dated at 12 to 6 Ma (Simpson 1947; Villarroel 1983; Carlini

et al. 1997). This view was radically modified when a new study of these taxa from northern South America indicated that they actually represented the first stages in the cladogenesis of the Glyptodontinae (Carlini et al. 2008b). Consequently, it is highly probable that this clade originated at those lower latitudes, and not in southern areas as originally believed. Another direct consequence of this reanalysis is that the Propalaehoplophorinae are now restricted to the Late Oligocene and Miocene of Argentine Patagonia.

During the Pliocene (5–1.8 Ma), the glyptodontines were represented by the genera *Glyptodontidium* and *Paraglyptodon* (3.5–1.8 Ma), with only southern records so far. Suggestively, as we have mentioned above, the first records of this clade in southernmost South America coincide with the maximum development of the southern plains, which ranged in time from 11 Ma to 3 Ma (see Pascual and Bondesio 1982). These vast plains probably occurred from Venezuela to Patagonia, especially during the Late Miocene–Pliocene (Ortiz-Jaureguizar and Cladera 2006), when the Glyptodontinae are recorded in southern areas. Thus, it is possible to hypothesize that these large open areas favored dispersion of the Glyptodontinae toward higher southern latitudes, by way of "para-Andean" biogeographical corridors (Carlini and Zurita 2007).

At some point during the Pliocene, when the definitive land connection between North and South America was established, these glyptodontines (quite probably, one of the groups that occupied northern South America) were part of the GABI (Gillette and Ray, 1981). Thus the records of the Late Pliocene and the Pleistocene of North America include the genus *Glyptotherium* with five species, namely, from oldest to most recent: (1) *G. texanum* Osborn (Late Pliocene), distributed in the southern United States; (2) *G. arizonae* Gidley (Late Pliocene–Early Pleistocene), also with records in the south of the U.S.; (3) *G. floridanum* (Simpson) (Late Pleistocene), with numerous records in central-south and southeastern U.S., and in central and south-central Mexico; (4) *G. mexicanum* (Cuatáparo and Ramírez) (Late Pleistocene), known only from its type specimen, from south-central Mexico; and (5) *G. cylindricum* (Brown) (Late Pleistocene), also known only from its holotype, found in central-western Mexico (Gillette and Ray 1981). The particular situation of the two latter species, which are morphologically very similar to each other, has led some paleontologists to suspect that they are indeed synonymous.

Glyptotherium was also distributed in Central America, since its presence has been mentioned by some authors for the Late Pleistocene of Panama and Honduras (Webb and Perrigo, 1984) and for the Pleistocene (probably Middle Pleistocene) of El Salvador (Cisneros et al. 2001; Cisneros 2005). In summary, the latitudinal distribution of the genus ranged from 36° N to 13–14° N. Consequently, their geographical range was limited to North America (where the genus could have arisen) and Central America.

Meanwhile, in the Pleistocene of South America, the glyptodontines also underwent important diversification and radiation, represented by the genus *Glyptodon* Owen with nearly thirteen recognized species, although some of these are probably invalid. This uncertainty exists because, unlike the North American species, whose validity has been recently reevaluated (see Gillette and Ray 1981), the South American forms are in urgent need of systematic revision.

In fact, from a biogeographical viewpoint, *Glyptodon* is the glyptodont genus with the greatest latitudinal distribution, including records in Argentina (see Ameghino 1889; Carlini and Scillato-Yané 1999; Tauber and Palacios 2008, among others); Paraguay (Hoffstetter 1978; Carlini and Tonni 2000); Uruguay (Ubilla 1996; Ubilla and Perea 1999; Ubilla et al. 2004); Brazil (Bombin 1976; Oliveira 1999; Ranzi 2000, among others), Bolivia (Takai et al. 1984; Marshall and Sempere 1991; Werdelin 1991), Peru (Pujos and Salas 2004); Ecuador and probably Colombia (Marshall et al. 1984), and Venezuela (Rincón, White, and McDonald 2008). Remarkably, *Glyptodon* species are common in the "para-Andean" region and in the eastern coast, but scarce in the Amazon region (Pujos and Salas 2004). Unlike the North American form (*Glyptotherium*), whose oldest record dates from around 2.6 Ma, in the state of Arizona (southern USA), the first records of *Glyptodon* are restricted to 1.07 Ma (Soibelzon, Zurita, and Carlini 2006; Soibelzon et al. 2008).

In this scenario, it has always been assumed that, while *Glyptodon* was restricted to South America, *Glyptotherium* was strictly limited to North and Central America. Similarly, the GABI was interpreted as a unidirectional process in which glyptodonts simply migrated toward North America. However, new discoveries from the latest Pleistocene of Venezuela, in sediments dated at approximately 15–12 ka (Carlini, Zurita, and Aguilera 2008a) and from the Pliocene (ca. 3.6–3.9 Ma) of Mexico (Carranza-Castañeda and Miller 2004; Flynn et al. 2005), have modified this scenario, suggesting interesting implications for the GABI.

In Venezuela, the Pleistocene records of glyptodonts are common, and they have been traditionally assigned to genus *Glyptodon* (see Casamiquela 1979; Bocquentin Villanueva 1982; Rincón, White, and McDonald 2008, among others); however, a new study of these materials indicated that these forms actually correspond to genus *Glyptotherium*, and that they are very similar to *G. cylindricum*, a species with more recent appearance and more southward records. From a biogeographical perspective, these findings from Venezuela, which also represent the first records of *Glyptotherium* in South America, strongly suggest that this case involves a group emigrating from South America during the Pliocene, diversifying in North America, and later, at some point in the Late Pleistocene, migrating back into South America.

The migratory processes of these cingulates could have been facilitated by the existence of some type of biogeographical corridor of open environments, which would have hypothetically connected the Florida

peninsula with the current territories of Mexico, Central America, and northernmost South America (Morgan and Hulbert 1995; Webb 2006). The development of these corridors must have reached its highest expression during the Last Glacial Maximum (ca. 21–18 ka BP), when the sea level descended 120 to 140 meters below its current condition (Rabassa, Coronato, and Salemme 2005).

Apart from this, it had always been supposed that the definitive connection between both Americas occurred at approximately 2.7 Ma, since this is the age of the earliest records of South American immigrants in the southern United States (Webb 2006). However, the discovery of glyptodontines in central Mexico, dated at 3.9 Ma, raises new questions about the actual timing of this land connection, since it would be reasonable to think that heavy armored forms such as these glyptodonts were poor swimmers. Another immediate question is why there is a difference of more than one million years between the oldest South American fauna recorded in the southern United States and the one from central Mexico.

The Pampatheres during GABI

As mentioned above, the pampatheriids (along with the dasypodids and glyptodonts) were the cingulates that participated in the GABI (Stehli and Webb 1985), and their records in North America range from the Late Pliocene to the Late Pleistocene (Woodburne, Cione, and Tonni 2006). The two Pleistocene genera are *Holmesina* and *Pampatherium*, which not only are morphologically distinct, but also seem to have been adapted to somewhat different environments, at least in South America. While the species of *Holmesina* (*H. occidentalis*, *H. majus*, *H. paulacoutoi*) would have lived in relatively humid conditions, the evidence suggests that the species of *Pampatherium* (*P. humboldtii* and *P. typum*) would have evolved in arid or semi-arid colder conditions (De Iuliis, Bargo, and Vizcaíno 2000).

In South America, two Mio-Pliocene genera of pampatheriids, which could be related to the origin of the two Pleistocene genera, have been recognized. *Vasallia* seems to be more closely linked to *Pampatherium*, whereas the genus *Kraglievichia* is morphologically closer to *Holmesina* (Scillato-Yané et al. 2005).

Based on the hypothetical relationships summarized above, a hypothetical biogeographical scenario can be advanced not unlike the one proposed for the Glyptodontidae. The evidence suggests that *Kraglievichia* (or a related taxon) would have migrated to North America during the GABI, and there the genus *Holmesina* would have differentiated with a single species, *H. septentrionalis.* Later, at some point during the Late Pleistocene (and quite possibly in connection with a glacial period, as in the case of the Glyptodontinae), this genus would have entered South America using two main migratory routes: one parallel to the Andes mountain range (*H. occidentalis*) and another following the Atlantic

coast (*H. majus*). The constant climatic-environmental fluctuations of the Pleistocene (see Clapperton 1993; Tonni et al. 2003) would have stimulated the cladogenesis of the most derived *Holmesina* species: *H. paulacoutoi*.

In this context, the genus *Pampatherium* had been assumed to be strictly South American, just like *Glyptodon*. However, in the case of pampatheriids, and in contrast with the glyptodontines, some recent discoveries assignable to *Pampatherium* in the Pleistocene of Mexico could indicate that pampatheriids underwent two emigration processes: the first, at some point during the Pliocene, which would have involved *Kraglievichia* or a related form that gave rise to *Holmesina* in North America, and a later migratory process (possibly during the Early or Middle Pleistocene), which involved a species of *Pampatherium*.

The Dasypodids during GABI

Unfortunately there are still only poor records of dasypodids in the Pliocene of Venezuela, which would allow us to establish which clades participated in the GABI. Only recently have the first remains of fossil Dasypodidae been found, which confirm the presence of this clade in Falcón state, Venezuela. The remains come from the San Gregorio Formation (a Pliocene unit younger than the Codore Formation), and are probably represented by the genus *Propraopus*, a taxon that has an ample latitudinal distribution, ranging from 38° S to 12° N, taking into account this record.

Surprisingly, the two Dasypodidae of largest latitudinal distribution, past or current, are represented by the dasypodines *Dasypus* and *Propraopus*. In fact, in the recent fauna of North America the genus *Dasypus* (*D. novemcinctus*) reaches up to 34° N, and its distribution has greatly increased in historical times.

The Evolutionary and Biogeographical History of Glyptodontinaes and Pampatheriids

As we have discussed, the latest finds from northern Venezuela, along with a reanalysis of the remains from Colombia, have brought about a new interpretation of the evolutionary and biogeographical history of one of the major groups of glyptodonts, the Glyptodontinae (glyptodontines). This can be summarized in the following points:

1 The morphological evidence suggests that the glyptodonts from the Middle Miocene–Pliocene (ca. 12–5 Ma) of northernmost South America (Colombia and Venezuela) do not belong to the subfamily Propalaehoplophorinae, but actually represent the first stages in the cladogenesis and later dispersion of the Glyptodontinae.

2 As a consequence of this, the Propalaehoplophorinae are restricted to southernmost South America (Argentine Patagonia). Likewise, the oldest records of Glyptodontinae are those from the Miocene–Pliocene of the current territories of Colombia and Venezuela.

3 The oldest records of Glyptodontinae in southernmost South America, from the latest Miocene and Pliocene of Argentine provinces Catamarca and Tucumán, partly coincide with the peak of the "Age of Southern Plains." This great latitudinal extension of open savanna environments could have stimulated the southward dispersal of these glyptodonts, by way of "biogeographical corridors," as proposed for other mammals.

4 At some point during the Pliocene, the glyptodontines (probably together with the glyptatelines) passed onto Central and North America, along with many other mammalian orders. At present, *Glyptotherium* is the only genus recorded in those areas.

5 The presence of *Glyptotherium* (*cf. G. cylindricum*) in the latest Pleistocene (ca. 14 ka) of Venezuela (Falcón state) suggests an entry of these glyptodontines into South America at some point during the Late Pleistocene, probably associated with "biogeographical corridors" that could have formed during the glacial periods, as proposed for other Cingulata (e.g., Pampatheriidae).

A similar bidirectional migratory pattern has been proposed for another Cingulata group, the pampatheriids; although this pattern is similar to the one advanced for glyptodontines, it differs in some aspects. The main points of this proposal are as follows:

1 During the GABI, the pampatheriids (like the glyptodontines) migrated into Central and North America. The genus *Holmesina*, with the species *H. septentrionalis*, would have evolved in these regions.

2 Later, this genus reentered South America, following two routes: one "para-Andean" and another parallel to the eastern coast. The cyclical climatic-environmental fluctuations that occurred during the Pleistocene would have triggered speciation processes that gave rise to endemic South American species.

4 Finally, and possibly during the Early Pleistocene–Middle Pleistocene lapse, another genus (*Pampatherium*) would have migrated toward North America, originating the species *Pampatherium mexicanum*.

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New Glyptodont from the Codore Formation (Pliocene), Falcón State, Venezuela, its relationship with the *Asterostemma* problem, and the paleobiogeography of the Glyptodontinae

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with 3 figures

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Abstract: One of the basal Glyptodontidae groups is represented by the Propalaehoplophorinae (late Oligocene – middle Miocene), whose genera (*Propalaehoplophorus, Eucinepeltus, Metopotoxus, Cochlops*, and *Asterostemma*) were initially recognized in Argentinian Patagonia. Among these, *Asterostemma* was characterized by its wide latitudinal distribution, ranging from southernmost (Patagonia) to northernmost (Colombia, Venezuela) South America. However, the generic assignation of the Miocene species from Colombia and Venezuela (*A.? acostae, A. gigantea*, and *A. venezolensis*) was contested by some authors, who explicitly accepted the possibility that these species could correspond to a new genus, different from those recognized in southern areas. A new comparative study of taxa from Argentinian Patagonia, Colombia and Venezuela (together with the recognition of a new genus and species for the Pliocene of the latter country) indicates that the species in northern South America are not Propalaehoplophorinae, but represent the first stages in the cladogenesis of the Glyptodontinae glyptodontids, the history of which was heretofore restricted to the late Miocene – early Holocene of southernmost South America. Accordingly, we propose the recognition of the new genus *Boreostemma* for the species from northern South America and the restriction of *Asterostemma* to the Miocene of Patagonia. Thus, the available data indicate that the Glyptodontinae would in fact have arisen in the northernmost regions of this continent. Their arrival to more southerly areas coincides with the acme of the "Age of Southern Plains". The Propalaehoplophorinae are geographically restricted to Patagonia.

Keywords: *Boreostemma pliocena* n. gen., n. sp. • Glyptodontinae • Propalaehoplophorinae • paleobiogeography • phylogeny • South America

Kurzfassung: Eine der basalen Gruppen der Glyptodontidae stellen die Propalaehoplophorinae (spätes Oligozän – mittleres Miozän) dar, deren Gattungen (*Propalaehoplophorus, Eucinepeltus, Metopotoxus, Cochlops* und *Asterostemma*) man zuerst aus dem argentinischen Patagonien kannte. Darunter ist *Asterostemma* durch eine weite latitudinale Verbreitung gekennzeichnet, welche sich vom südlichsten (Patagonien) zum nördlichsten (Kolumbien, Venezuela) Südamerika erstreckt. Allerdings wurde die Gattungszugehörigkeit der miozänen Arten Kolumbiens und Venezuelas (*A.? acostae, A. gigantea* und *A. venezolensis*) von einigen Autoren angezweifelt, die explizit die Möglichkeit in Betracht zogen, dass diese Taxa einer anderen Gattung angehören, die sich von der Gattung der südlichen Breiten unterscheidet. Ein neuer Vergleich der Taxa aus Patagonien, Kolumbien und Venezuela (zusammen mit einer neuen Gattung und Art aus dem Pliozän Venezuelas) zeigt, dass die Arten aus dem nördlichen Südamerika nicht zu den Propalaehoplophorinae gehören, sondern die ersten Stufen in der Kladogenese der glyptodontinen Glyptodontidae darstellen. Deren Geschichte war bislang auf das späte Miozän – frühe Holozän des südlichsten Südamerikas beschränkt. Dementsprechend stellen wir hier die neue Gattung *Boreostemma* für die Arten des nördlichen Südamerikas auf; *Asterostemma* wird auf das Miozän Patagoniens beschränkt. Die Datenlage deutet somit darauf hin, dass Glyptodontinae sich tatsächlich im nördlichsten Teil Südamerikas entwickelten. Ihr Auftreten in den südlichen Gebieten fällt mit dem Höhepunkt des „Zeitalters der südlichen Ebenen" zusammen. Die Verbreitung der Propalaehoplophorinae wird geographisch auf Patagonien beschränkt.

Schlüsselwörter: *Boreostemma pliocena* n. gen., n. sp. • Glyptodontinae • Propalaehoplophorinae • Paläobiogeographie • Phylogenie • Südamerika

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Introduction

Among the particular palaeofauna that inhabited South America during much of the Cenozoic, the cingulate superfamily Glyptodontoidea are one of the most conspicuous groups; several authors have recognized more than 65 genera during their diversification (late Eocene – early Holocene) (see MCKENNA & BELL 1997). In this context, the Glyptodontidae Propalaehoplophorinae (sensu CASTELLANOS 1932) are among the best characterized basal clades (together with the Glyptatelinae; late Eocene – late Miocene; SCILLATO-YANÉ 1977; CARLINI et al. 1997; VIZCAÍNO et al. 2003), and have been proposed by several authors as potential structural ancestors of later Glyptodontidae (SCOTT 1903–1904; SCILLATO-YANÉ 1977).

The propalaehoplophorine glyptodonts are morphologically characterized by the following traits: a) low elongated skull, partly resembling those of dasypodid cingulates; b) dorsal carapace with mobile bands on the lateral margins (no less than 6 rows in *Propalaehoplophorus* and *Cochlops*), which is probably the primitive condition for the Glyptodontidae; c) ornamentation of dorsal carapace osteoderms consisting of a polygonal central figure completely encircled by a row of smaller peripheral figures, forming a rosette; d) caudal armor formed by a series of rings (generally four to six), each ring formed by two rows of osteoderms, followed by a short caudal tube; e) five digits in both fore- and hindlimbs; f) first three upper and lower molariforms simple, subcircular or subelliptic in transversal section. Many of these characters could be considered primitive; however, some of them (c–d) do not occur in the Glyptatelinae, or there is no evidence of their occurrence.

From a chronological viewpoint, the subfamily Propalaehoplophorinae is first recorded during the Deseadan (late Oligocene) (SCILLATO-YANÉ 1977), a time of remarkable increase in glyptodontid diversity. The Deseadan also marks the end of the records of Glyptatelinae at high latitudes; however, they persist in more northern areas, until the middle Miocene in Colombia (CARLINI et al. 1997; VILLARROEL & CLAVIJO 2005) and until the late Miocene in Uruguay (VIZCAÍNO et al. 2003). They might even have occurred in the early Pleistocene of North America (MCKENNA & BELL 1997).

During the Colhuehuapian (early Miocene), and especially during the Santacrucian (early Miocene), the Propalaehoplophorinae show great diversification, evidenced in the recognition of five genera and eight species in Argentinian Patagonia during this latter South American Land Mammal Age (SALMA): *Propalaehoplophorus* AMEGHINO, 1887 (*P. australis* and *P. minor*), *Cochlops* AMEGHINO, 1889 (*C. muricatus* and *C. debilis*), *Eucinepeltus* AMEGHINO, 1891 (*E. complicatus* and *E. petestatus*), *Metopotoxus* AMEGHINO, 1898 (*M. anceps*), and *Asterostemma* AMEGHINO, 1889 (*A. depressa*) (see SCOTT 1903–1904). In this context, a recent phylogenetic analysis of the southern Propalaehoplophorinae (*Propalaehoplophorus*, *Eucinepeltus*, *Metepotoxus*, and *Cochlops*) has suggested that these taxa can be regarded as a monophyletic group (FERNÍCOLA 2006).

The "Friasian" lapse (middle – late Miocene) (which comprises three successive "faunas", Friasian s. s., Colloncuran and Mayoan; SCILLATO-YANÉ & CARLINI 1998) signals the beginning of the Panaraucarian Faunal Cycle, Protoaraucarian Subcycle (Friasian – Chasicoan, of PASCUAL & ORTIZ JAUREGUIZAR 1990; PASCUAL et al. 1996). The Xenarthra, especially the large cursorial Tardigrada (such as Megatheriidae, Mylodontidae, and Scelidotheriinae; see MC DONALD 1987) become larger and more frequent during this period (PASCUAL et al. 1996; ORTIZ JAUREGUIZAR & CLADERA 2006). This phenomenon could be associated with the progressive aridization of the Southern Cone of South America, as a consequence of the Andean-Patagonian Orogeny (see PASCUAL & BONDESIO 1982; PASCUAL 1984; PASCUAL et al. 1984; ORTIZ JAUREGUIZAR & CLADERA 2006; TONNI & CARLINI in press). This climatic-environmental context characterizes the last southern records of Propalaehoplophorinae (*Propalaehoplophorus*? and *Eucinepeltus*) (BONDESIO et al. 1980), as well as the first records of Hoplophorinae, with the tribes Hoplophorini? (*Eonaucum colloncuranun* SCILLATO-YANÉ & CARLINI, 1998) and Palaehoplophorini (*Palaehoplophorus* AMEGHINO and *Palaehoplophoroides* SCILLATO-YANÉ & CARLINI) (PAULA COUTO 1979; SCILLATO-YANÉ & CARLINI 1998).

Argentinian Patagonia seems to have been, at least until the "Friasian" (middle to late Miocene), the geographic location where the cladogenesis and radiation of this group is best recorded (PASCUAL & ODREMAN RIVAS 1973; PASCUAL et al. 1984), considering the good record of cingulates in the area (SCILLATO-YANÉ 1986). Furthermore, PASCUAL et al. (1984) and PASCUAL & ODREMAN RIVAS (1973) went so far as to propose this territory as a center of radiation and cladogenesis.

Recently, other possible evolutionary scenarios have been proposed for the Cingulata at lower latitudes. These hypotheses are especially supported by fossil remains from the Honda Group ("Friasian") in the fossil locality of La Venta, Colombia (CARLINI et al. 1997). Several taxonomic and paleobiogeographic differences between these materials and isochronous Patagonian paleofaunas support these hypotheses. These include the remarkable survival of a representative of the glyptateline Glyptodontidae (*Neoglyptatelus originalis*) with very primitive characters (CARLINI et al. 1997), as well as records of astegotheriine, dasypodine, and tolypeutine Dasypodidae, which are absent in Patagonia; in contrast, representatives of Peltephilidae, Euphractini, and Stegotheriini occur in the latter region (CARLINI et al. 1997).

Within this paleobiogeographic context, the Mio-Pliocene glyptodontid fauna in northern South America (Colombia and Venezuela), which remained unknown until the mid-1940s (see SIMPSON 1947), seems to agree with this hypothesis. Traditionally, all the Miocene glyptodonts from this area were included within the subfamily Propalaehoplophorinae, and more precisely, within the genus *Asterostemma*. Thus, three species have been described, *A. venezolensis* SIMPSON, 1947, for the (middle?) Miocene of Venezuela, and *A.*? *acostae* VILLARROEL, 1983 and *A. gigantea* CARLINI et al., 1997, for the middle Miocene (Laventan SALMA) of Colombia. The inclusion of these taxa in the southern genus *Asterostemma* was accepted by most authors, though with the explicit acknowledgment that these taxa could in fact represent a new genus, different from the ones traditionally recognized for the Patagonian Miocene (i.e., *Propalaehoplophorus*, *Eucinepeltus*, *Metopotoxus*, *Cochlops,* and *Asterostemma*) (see SIMPSON 1947: 9; VILLARROEL 1983: 30; CARLINI et al. 1997: 223).

In this contribution we present a new Glyptodontidae from the Codore Formation (Pliocene) of Falcón State, Venezuela (Fig. 1); concurrently, on the basis of both morphological and paleobiogeographic evidence, we propose the recognition of a new genus for all the Mio-Pliocene species recognized in northern South America (Colombia and Venezuela) that have tentatively been assigned to the southern genus *Asterostemma.*

The new Glyptodontidae described herein allows the proposal of a different evolutionary scenario for the species from northern South America; particularly, it allows us to elaborate a different hypothesis for the differentiation of the glyptodontine Glyptodontidae. This subfamily is known from the "Araucanian" (late Miocene – Pliocene) of NW Argentina, represented by *Glyptodontidium tuberifer* CABRERA, 1944, a species with dorsal carapace formed by thick osteoderms with the typical rosette comprising a central polygonal figure and several marginal figures in a single row. Although this character would be primitive among the propalaehoplophorine and glyptodontine glyptodonts, the morphology of the sulci that delimit the pattern on the exposed surface of the osteoderms is different in cross section. While in the southern Propalaehoplophorinae the cross section of these sulci is parabolic ("V"-shaped), in the Glyptodontinae it is quadrangular ("U"-shaped), with almost vertical sides and a wide, almost flat bottom. In addition, the carapace osteoderms of glyptodontines are relatively thicker than those of propalaehoplophorines, and the contact edges between successive osteoderms are definitely denticulated. In general, the section of these sulci and the thickness of osteoderms, together with the greater lobation of the anterior molariforms, are generally used to define the glyptodontine glyptodonts (HOFFSTETTER 1958; PASCUAL et al. 1966; PAULA COUTO 1979).

The history of the Glyptodontinae is rather particular, given that their earliest records (*Glyptodontidium tuberifer* from the "Araucanian"; late Miocene – Pliocene) are not very frequent or diverse in late Neogene sediments; only two species, *Paraglyptodon chapalmalensis* from the middle Pliocene (Chapadmalalan) of the Pampean region and *Paraglyptodon uquiensis* CASTELLANOS, 1953, from the middle – late Pliocene (late Chapadmalalan – Sanadresian) of the current territory of Jujuy province (see REGUERO et al. 2007), both from Argentina, have been described for that period. However, the Glyptodontinae become very frequent in southern sediments since the Ensenadan (late Pliocene – early Pleistocene; ca. 1.7 – 0.98 Ma) of the Pampean region, achieving both noticeable taxonomic richness and extensive latitudinal distribution that ranged from the south of Buenos Aires province to, probably, Venezuela (see MARSHALL et al. 1984; TONNI & SCILLATO-YANÉ 1997; RINCÓN 2006). Thus, approximately eight *Glyptodon* species have been recognized for the Pleistocene of southernmost South America (SOIBELZON et al. 2006; CARLINI & SCILLATO-YANÉ 1999).

Similarly, this subfamily is very well represented in North America since the early Blancan (ca. 2.6 Ma), that is, immediately after the establishment of a continuous Panamanian terrestrial connection (ca. 2.7 Ma), with the genus *Glyptotherium* (see CARLINI et al. 2008). However, recently CARRANZA-CASTAÑEDA & MILLER (2004) cited the presence of *Glyptotherium* OSBORN, 1903 in Pliocene sediments from central Mexico, dated by them at 3.9 Ma, although the generic assignation is not secure, given that the authors themselves (2004: 258) highlight the marked differences with respect to known *Glyptotherium* species. It would not be surprising, if these Mexican findings were to correspond in fact to a new taxon close to the one described here.

Abbreviations: AMNH, American Museum of Natural History, New York, USA; AMU-CURS, Colección de Paleontología de Vertebrados de la Alcaldía de Urumaco, Estado Falcón, Venezuela; M, m, upper and lower molariform respectively; GABI, Great American Biotic Interchange; ICNUNC, Instituto de Ciencias Naturales, Universidad Nacional de Colombia; IGM, Instituto de Geociencias y Minería, Colombia ; n/n, without official catalog number; SALMA, South American Land Mammal Age.

Geologic and stratigraphic context: the Codore Formation

The Codore Formation was recognized and described by HODSON (1926) in Falcón State, Venezuela, and assigned chronologically to the Pliocene s.l., while always considered older than the overlying San Gregorio Fm. from the late Pliocene (GONZALEZ DE JUANA et al. 1980). This geologic unit is divided into two (see LIDDLE 1946) or three (see REY 1990) members, according to different authors. Lithologically, it comprises a succession of ochraceous to dark brown sandstones with cross-stratification, and light-colored limolites with in-

Fig. 1. Map showing the locality where the type specimen of *Boreostemma pliocena* n. gen., n. sp. was recovered.

tercalated carbonatic levels of varying thickness. The depositional environment has been interpreted by REY (1990) as characteristic of a distal fan-delta, with an alluvial plain associated with small meandering channels, and some brief intervals of marine invasion halfway through the sequence. The presence of palynomorphs allows to infer subhumid to dry climate throughout the entire deposition of the Codore Fm. (LINARES 2004). The sequence is about 800 m thick and comprises sediments concordant with the underlying Urumaco Fm. (late Miocene). Recently, LINARES (2004), on the basis of the mammalian fauna, has assigned an age corresponding to the Montehermosan SALMA (late Miocene – early Pliocene) to the El Jebe Member of Codore Fm., and suggested a probable age of 6 Ma for the contact between the Urumaco and Codore formations.

Systematic paleontology

Xenarthra COPE, 1889
Cingulata ILLIGER, 1811
Glyptodontoidea GRAY, 1869
Glyptodontidae GRAY, 1869
Glyptodontinae GRAY, 1869

Boreostemma n. gen.

Etymology: *Boreos* from the Latin "borealis" "from the North", in reference to its geographical distribution, restricted to northern South America, + "*stemma*" ending of *Asterostemma*, austral genus to which it was previously wrongly assigned.
Type species: *Boreostemma pliocena* n. gen., n. sp., from the Codore Formation, El Jebe Member, Pliocene, northern Venezuela.
Referred species: The type species and *Asterostemma venezolensis* SIMPSON, 1947 (middle? Miocene, eastern Venezuela), *Asterostemma? acostae* VILLARROEL, 1983 [sic]

(middle Miocene, Huila Department, Colombia), *Asterostemma gigantea* CARLINI et al., 1997 (La Victoria Formation, Honda Group, middle Miocene; Huila Department, Colombia).

Diagnosis: Small to medium sized Glyptodontinae, ranging in size from that of *Propalaehoplophorus australis* to *Eucinepeltus crassus*. Osteoderms arranged in transverse bands more regular than in Propalaehoplophorinae, with rugose and very punctate surface. Central figure polygonal, in a more central position. Sulci surrounding adjacent figures wide, which has (in cross section) nearly vertical walls and wide bottom, which we call "U"-shaped, contrasting with the "V"-shaped sulci of Propalaehoplophorinae and Hoplophorinae hoplophorini with convergent walls and strait bottom. Area of contact and articulation of adjacent osteoderms strongly denticulate, with deep osseous interdigitating projections. Generally, a single series of peripheral figures in each osteoderm, morphologically simpler than those of Glyptodontidae Propalaehoplophorinae. Peripheral figures of two or three adjacent osteoderms forming composite figures. Caudal rings imbricated, formed by a single row of osteoderms. Posterior region of caudal tube with slightly imbricated osteoderms, more similar to the caudal tube of Dasypodidae than to those of known Propalaehoplophorinae. Dorsal carapace formed by larger, thicker and fewer osteoderms than in Propalaehoplophorinae.

Boreostemma pliocena n. sp.

Figs. 2A–D, 3

Etymology: "*pliocena*" from Pliocene, the age of the Codore Formation, Venezuela.

Holotype: Thirty complete, associated osteoderms, some fragmentary osteoderms, and a fragment of the palate with partial alveoli of M 5–7.

Type locality: Road to Tío Gregorio locality, Urumaco, Estado Falcón, Venezuela, 11° 15' 35" N and 70° 17' 30" W (Fig. 1).

Stratigraphic range and geochronologic age: El Jebe Member of the Codore Formation, Pliocene.

Diagnosis: Osteoderms of dorsal carapace very large, with extremely punctuate dorsal surface, very similar in this respect to *Boreostemma gigantea, B. acostae, B. venezolensis, Glyptodontidium tuberifer* and *Paraglyptodon uquiensis*, and contrasting with the condition observed in the southern Propalaehoplophorinae (*Propalaehoplophorus, Eucinepeltus, Metopotoxus,* and *Asterostemma*), which have a smoother exposed surface. Punctuation especially concentrated in a slight central concavity at each central figure, more visible in the largest (dorsal and posterodorsal) osteoderms. Sulci dividing the central figure from the peripheral ones, and the latter from each other, wide and shallow, as in *Glyptodontidium tuberifer, Paraglyptodon uquiensis and P. chapalmalensis*; hair follicle (?) pits well developed and situated (as in most of the Glyptodontidae with this rosette ornamentation pattern) at the intersections between the sulcus surrounding the central figure and the sulci between peripheral figures. Caudal rings imbricated, formed by a single row of osteoderms. Caudal ring osteoderms with barely marked central figure and without signs of peripheral figures, differing from *Propalaehoplophorus australis* and *Cochlops muricatus* (propalaehoplophorines whose osteoderms are well-known), in which the central figure is clearly visible and a row of peripherals is present at the proximal edge. Posterior upper molariforms (at least M5–M7) very close to each other, with almost no separation, differing from those of Propalaehoplophorinae, in which the separation between molariforms increases disto-proximally. Ornamentation of cephalic shield osteoderms similar to that of dorsal carapace, as in *Propalaehoplophorus australis* and the hoplophorine Hoplophorinae *Neosclerocalyptus* PAULA COUTO, 1957, and very different from that of *Eucinepeltus complicatus* and *Metopotoxus laevatus*, which show no signs of rosette ornamentation.

Description and assignation of material

Palate: This is a posterior fragment with part of the alveoli for molariforms M6 and M7 on the left side, and the last alveolar lobe of M6, that of M7 and the first of M8 on the right side (Fig. 3). It is 53.5 mm long and 35 mm wide. The entire surface of the palate is pierced by foramina that are particularly evident on the midline. There are also six large foramina at the level of the first lobe of M7, at the limit between M7 and M8, and at the limit between the first and second lobes of M8. On the right side, these foramina open at the level of the last lobe of M6, the second lobe of M7 and the first lobe of M8. Apart from this, the particular arrangement of the alveoli for the last molariforms shows virtually no separation between M7 and M8. This trait is clearly different from the condition in Propalaehoplophorinae, in which the separation between successive molariforms increases disto-proximally. On the other hand, the middle lobe seems to be more inclined with respect to the longitudinal axis of the palate than in *Propalaehoplophorus, Asterostemma, Eucinepeltus*, and *Cochlops*, in which this lobe is approximately at straight angles to the anteroposterior axis of the dental series.

Osteoderms: Numerous osteoderms from the dorsal carapace, as well as some from the cephalic shield, have been preserved. They are categorized into five groups according to their location on the dorsal carapace.

a) First group: these osteoderms correspond to the dorsal or postero-dorsal region of the carapace (Fig. 2A). The larger ones are 51 mm by 47 mm in diameter, and 14 mm thick, while the smaller are 39 mm by 33 mm and 10 mm, respectively. Each osteoderm has five or six sides (in most) which are relatively isodiametric, with extremely punctate dorsal surface, as in *Glyptodontidium tuberifer, Paraglyptodon uquiensis,* and *Boreostemma acostae* (n. comb.). The central figure is poly-

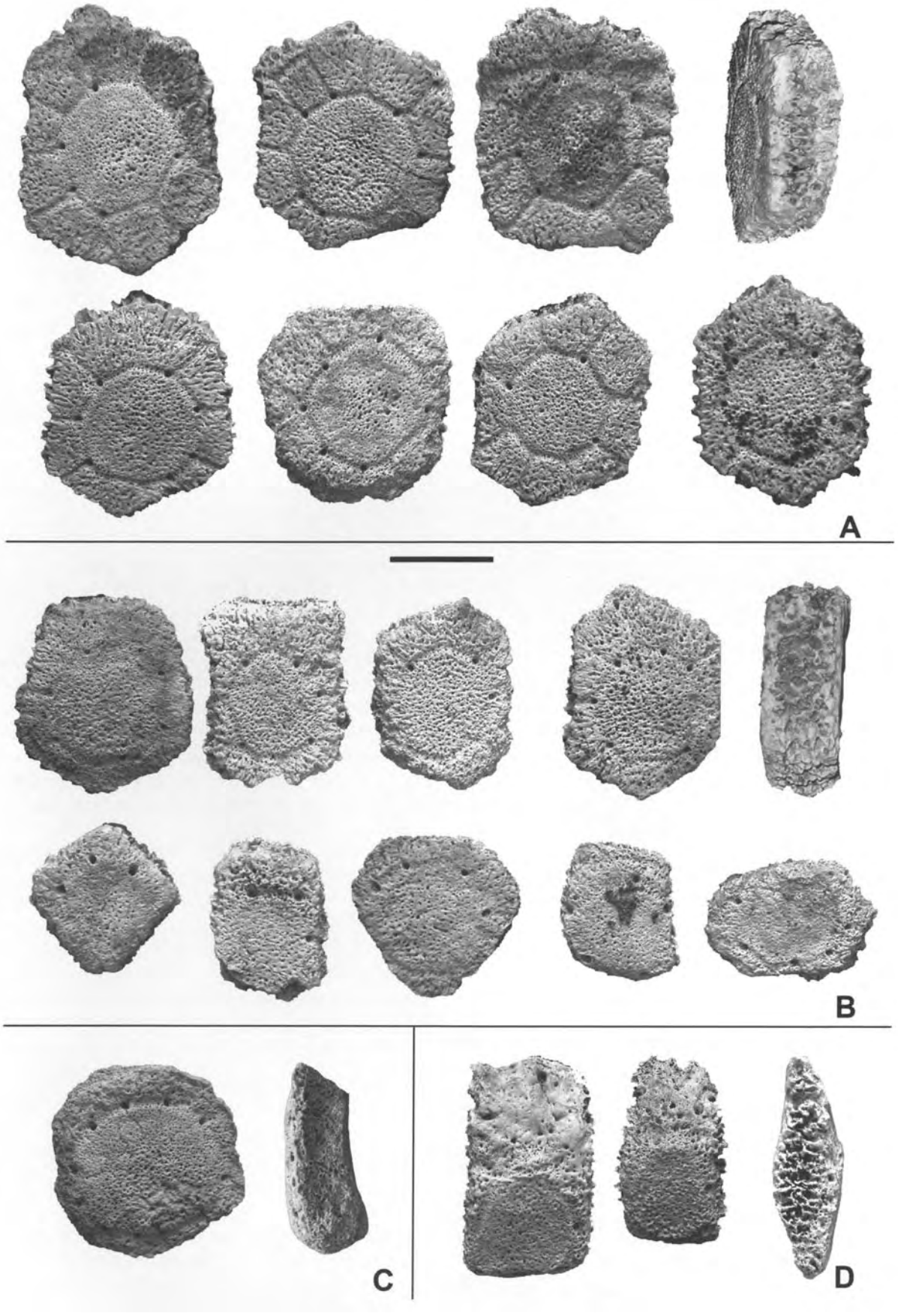

Fig. 2. *Boreostemma pliocena* n. gen., n. sp. **A**: Osteoderms corresponding to the dorsal or postero-dorsal region of the carapace (seven in external view, one in lateral view). **B**: Osteoderms from the sides of the carapace (nine in external view, one in lateral view). **C**: One osteoderm from the cephalic shield (external and lateral views). **D**: Osteoderms from the caudal rings (two in external view, one in lateral view). – Scale bar = 2 cm.

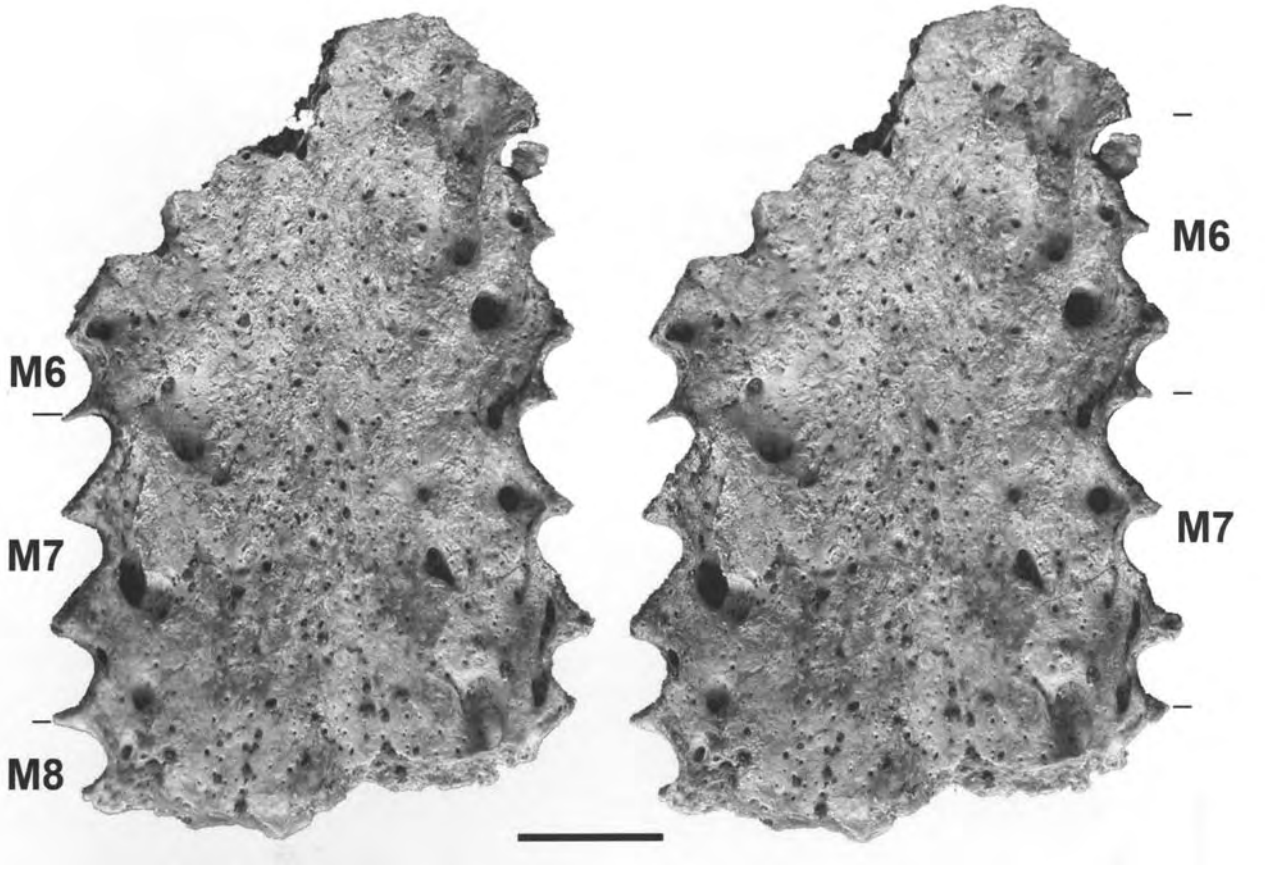

Fig. 3. *Boreostemma pliocena* n. gen., n. sp. Palate: stereopairs of a posterior fragment with part of the alveoli for molariforms M6 and M7 on the left side, and the last alveolar lobe of M6, that of M7 and the first of M8 on the right side. – Scale bar = 2 cm.

gonal, with the number of sides coinciding with the number of peripheral figures. The central figures of the larger osteoderms are between 23.5 by 21 mm, and 25 mm by 19 mm. The figures of the smaller osteoderms are 19 mm by 18 mm. The dorsal surface of the central figures is slightly elevated with respect to the peripheral ones, particularly in the larger osteoderms, whereas it is flat in the smaller ones. As mentioned above, the entire surface of each central figure is densely punctate (although much less than in *Glyptodon* and *Glyptotherium*, in which the surface of the osteoderms is definitely rugose), but this condition becomes especially evident at its central area, which bears larger-diameter foramina located in a small concavity, somewhat similarly to the morphology of *Boreostemma acostae*. As in the previous case, this concavity is more conspicuous in the larger osteoderms. Each central figure is surrounded by a row of eight to ten peripherals, 4- or 5-sided, well developed and very angular. The number of peripherals seems to be lower when compared to the southern Propalaehoplophorinae forms; the latter may have up to twelve or thirteen peripherals (see SCOTT 1903–1904). The entire surface of these figures is clearly punctate, although the punctuations situated toward the periphery are somewhat radial in appearance (as they become oblique instead of perpendicular to the surface), as observed in some osteoderms of *Paraglyptodon uquiensis* and *Paraglyptodon chapalmalensis* (see ROVERETO 1914; CASTELLANOS 1953). A conspicuous foramen appears in some of the intersections between the sulcus that delimitates the central figure and the radial sulci; there are three to eight of these foramina. The sulci separating the central figure from the peripherals, and the radial sulci between peripherals are wide, shallow, with nearly flat bottom, and morphologically similar to those of *Glyptodontidium tuberifer*. The sulci are similar in *Paraglyptodon uquiensis* and *P. chapalmalensis*, although in these latter species the sulci are deeper and somewhat similar to those of the genera *Glyptodon* and *Glyptotherium*.

The ventral surface of the osteoderms may be flat or slightly concave at the center. One to nine foramina are visible on this surface; generally the largest (one or two of them) occupy a central position while the rest are arranged peripherically in a circular pattern.

b) Second group: osteoderms from the sides of the carapace (Fig. 2B). These are rectangular with a disto-proximal long axis, and have four to six sides. The largest are 37.5 mm by 23 mm and 14 mm thick, while the smallest are 28 mm by 21 mm and 9.5 mm thick. The entire exposed surface is visibly punctate, as in the dorsal and posterodorsal osteoderms. The central figure is flat, with subelliptical to subcircular outline, and unlike the dorsal osteoderms, does not show a concave area with larger fo-

ramina. The eight or nine peripheral figures are less developed than in the dorsal osteoderms, and the lateral ones are smaller. As in the Propalaehoplophorinae and the most primitive hoplophorine Hoplophorinae (i.e., *Eosclerocalyptus tapinocephlaus* and *E. proximus*), the anterior peripheral figures are larger than the posterior ones. The central and radial sulci are only slightly marked, and the number of foramina ranges between three and six.

c) Third group: formed by very small osteoderms of the dorsal carapace, possibly corresponding to the extreme antero-lateral and postero-lateral regions of the carapace. These osteoderms are quadrangular to hexagonal, and measure from 24 mm by 24.5 mm and 11 mm thick, to 25 mm by 23 mm and 8.5 mm thick. The entire dorsal surface has the same characteristics described above for other osteoderms, with three to five well-developed hair follicle (?) pits at the intersections between the sulcus surrounding the central figure and the sulci between peripheral figures, but in this case there is no differentiation between central and peripheral figures.

d) Fourth group: osteoderms from the caudal rings (Fig. 2D). These are clearly rectangular with a disto-proximal long axis. The largest osteoderms are 44 mm by 23. 5 mm and 12 mm thick, while the smallest one is 34 mm by 20 mm and 9 mm thick. Each osteoderm shows two well-defined areas: a distal area with a flat exposed surface, and a proximal area with an extremely rugose irregular surface, the latter corresponding to the area of contact and articulation with the adjacent osteoderm. The surface of the distal area is flat and punctate, although a disto-proximally elongated small convexity was observed in the center of one of the osteoderms studied. In addition, these osteoderms bear a very weak sulcus that delimits a subcircular central figure, although there are no peripheral figures; this central figure is 16 mm long by 15 mm wide in the smallest osteoderms and 19 by 17 mm in the largest ones. This particular morphology differentiates this taxon from *Propalaehoplophorus australis* and *Cochlops muricatus*, as both have a clearly visible central figure and a row of peripherals at the proximal margin. A series of foramina, larger than those of the dorsal carapace osteoderms, is evident at the lateral and posterior margins.

Likewise, the proximal contact area is depressed toward its proximal end, and has a very rugose surface with large foramina. In lateral view, the osteoderms are maximally thick at their center and become thinner toward the edges, particularly at the proximal margin.

e) Fifth group: only one osteoderm from the cephalic shield is well preserved. It is somewhat similar to those of *Propalaehoplophorus*, and clearly different from those of *Eucinepeltus* and *Metopotoxus* (Fig. 2C). The osteoderm is relatively isodiametric, 36 mm by 35 mm and 13 mm thick. The central figure is subcircular (24 mm by 27 mm) and slightly elevated with respect to the peripheral figures. As in the largest dorsal carapace osteoderms, the largest punctuations are concentrated in the center of the figure, although with a slight tendency to occupy one of the margins. The twelve peripheral figures are asymmetrically developed, and largest and thickest at the margin/border. Eleven hair follicle (?) pits are clearly visible.

The ventral surface of the osteoderm is notably concave at its center; much more so than any osteoderm from the first group, with three large foramina at the area of maximum thickness.

The problem of the genus *Asterostemma* AMEGHINO in the context of the Glyptodontidae / Propalaehoplophorinae

All the genera of propalaehoplophorine Glyptodontidae (*Propalaehoplophorus*, *Asterostemma*, *Cochlops*, *Metopotoxus*, and *Eucinepeltus*) were originally recognized on the basis of materials exhumed from the early and middle Miocene (Colhuehuapan, Santacrucian, and Friasian ages) of Argentinian Patagonia (see AMEGHINO 1889, 1891; LYDEKKER 1894; SCOTT 1903–1904; RUSCONI 1946, among others). Osteoderm ornamentation in this subfamily is characterized by a central figure encircled by a row of more-or-less angular peripheral figures, producing a characteristic rosette pattern (HOFFSTETTER 1958; PAULA COUTO 1979) that remains almost unchanged in later groups (e.g., hoplophorine Hoplophorinae; see ZURITA et al. 2005). This situation, together with the absence of isochronic records in more northern areas, led some authors to suggest that some of these Propalaehoplophorinae were the ancestral stock for the remaining Glyptodontidae lineages (SCOTT 1903–1904: 155). The diagnostic characters provided by AMEGHINO (1889: 822) for his genus *Asterostemma* seem to be highly variable within a single dorsal carapace, and occur also in the remaining Propalaehoplophorinae species (e.g., number of sides of osteoderms in the dorsal carapace, size of the central figure and development of peripheral figures). Later, SCOTT (1903–1904), as part of a systematic revision of Propalaehoplophorinae, upheld the validity of the genus, but recognized only one of the three species originally described by AMEGHINO (1889), namely *A. depressa*, as valid, whereas he synonymized *A. laevata* and *A. granata* with *Metopotoxus laevatus* and *Cochlops muricatus*, respectively (SCOTT 1903–1904). In addition, this author referred new materials, particularly an isolated caudal armor, to *A. depressa* (but without providing an extensive rationale for his decision). He also emphasized that: "The status of this genus is somewhat uncertain and more complete material is greatly to be desired...". (SCOTT 1903–1904: 154). Finally, RUSCONI (1946: 9–11), on the basis of six associated dorsal osteoderms, recog-

nized a poorly-diagnosed new species, *A. barraelense* RUSCONI, 1946, from the Miocene of San Juan province.

Recently, the genus *Asterostemma* was reported by GOIS-LIMA & COZZUOL (2005) and COZZUOL (2006) in the upper Miocene of Acre (Brazil). Unfortunately, this Glyptodontidae material consists of one isolated osteoderm (not illustrated), and consequently its generic identification is uncertain.

SIMPSON (1947) was the first to recognize and describe a new propalaehoplophorine in more northern regions, a species from the middle Miocene of Venezuela (Santa Inés Fm.) that he tentatively assigned to the genus *Asterostemma* AMEGHINO (*A. venezolensis* SIMPSON). However, such traits as the evidently more complex morphology of the first lower molariforms, which are greatly elongated anteroposteriorly, the absence of mobile bands in the antero-lateral region of the dorsal carapace, and the particular ornamentation of the osteoderms that delimit the caudal notch, do not occur in any of the southern taxa. This situation was recognized by SIMPSON himself (1947: 9), who stated that "There remains, however, the distinct possibility that the Venezuelan specimen belongs in a distinct genus not defined from the Argentine".

Later on, DE PORTA (1962) referred some isolated osteoderms from the middle Miocene of Colombia to SIMPSON's species (*A. venezolensis*) and to *Propalaehoplophorus*, but without explicit reasons for these assignations. In 1983, VILLARROEL recognized and described a new species from the Miocene of the same country, and, like SIMPSON (1947), he assigned it provisionally to the genus *Asterostemma* (*A.? acostae* VILLARROEL [sic]).

More recently, CARLINI et al. (1997) described a new species from the middle Miocene (Laventan) of Colombia, *A. gigantea*. Among the diagnostic characters, the large size and evident complexity of the second lower molariform, which tends to be trilobed, are remarkable. Contrastingly, molariform lobation of the southern forms is clearly defined from the third or fourth tooth. Following the ideas of SIMPSON (1947) and VILLARROEL (1983), CARLINI et al. (1997) stated that *"Asterostemma gigantea* is clearly different from species of *Propalaehoplophorus* AMEGHINO, *Cochlops* AMEGHINO, *Eucinepeltus* AMEGHINO, and *Metopotoxus* AMEGHINO. Regrettably, the carapace of the type species *A. depressa* from the early Miocene of Patagonia is very poorly known. Like VILLARROEL (1983), we cannot completely discredit the idea that the Propalaehoplophorinae from northern South America, including *A. venezolensis* SIMPSON, could belong to a new genus, distinct from *Asterostemma*. In this case, *Asterostemma* would have a geographic distribution limited to Patagonia. Into this new genus, we would include the species described herein."

Paleobiogeography and morphology of the propalaehoplophorine and glyptodontine Glyptodontidae: a new scenario

Within this paleobiogeographic and morphologic framework, a detailed analysis of the main traits that characterize the southern Propalaehoplophorinae forms indicates that most of these traits do not occur in the more northern Mio-Pliocene forms (from Colombia and Venezuela). Thus, the southern Propalaehoplophorinae are characterized by: **a)** first two upper and lower molariforms simple, with subcircular or subelliptical outline, and third molariform with slight indication of lobation in some species; **b)** in the dorsal carapace, the sulci separating the central figure from the peripherals (main sulcus) and these from each other (radial sulci) are "V"-shaped in transversal section, a morphology that is conserved in the hoplophorine Hoplophorinae; **c)** dorsal surface of the osteoderms smooth, without remarkable features and, in many cases, with anterior accessory peripheral figures; **d)** vestiges of imbrication between successive osteoderm rows in the most anterolateral region of the dorsal carapace (as in Dasypodidae; see SCOTT 1903–1904). In addition, the monophyly of the southern forms has been suggested by FERNÍCOLA et al. (2006), although the issue is problematic and there is no clear consensus about it.

As we have mentioned before, a new and more thorough examination has shown that this combination of characters does not occur in the taxa from northern South America, which have been traditionally included in subfamily Propalaehoplophorinae on the basis of the superficial similarity in the rosette ornamentation pattern of the dorsal carapace.

The type of *Boreostemma venezolensis* n. comb. (n/n) shows a notable antero-posterior elongation and greater complexity of the first two lower molariforms, absence of mobile bands in the lateral region of the carapace, and a particular ornamentation of the osteoderms adjacent to the caudal notch (SIMPSON 1947).

In *Boreostemma acostae* n. comb. (ICNUNC P-225-1) the dorsal carapace osteoderms have a strongly punctate dorsal surface, particularly in the middle of the central figure; in addition, the sulci separating the central figure from the peripherals are wide and shallow (see VILLARROEL 1983).

Other remarkable traits of *Boreostemma gigantea* n. comb. (IGM 250928) are the large body sized and a beginning of trilobation already in the second lower molariform, which is morphologically more complex than that of *B. venezolensis*, and much more so than in the southern taxa. In addition, the carapace osteoderms are thick and lack secondary peripheral figures (CARLINI et al. 1997).

Finally, *Boreostemma pliocena* n. sp. (AMU-CURS 158) differs from the southern forms by the greater size and thickness of its osteoderms with strongly punctate dorsal surface, by its caudal ring osteoderms

with the central figure only slightly marked and no trace of peripheral figures, and by having the posterior upper molariforms (at least M6–M8) very close to each other with almost no separation.

In addition to this particular set of characters occurring in these taxa, a detailed examination of the morphology of the sulci that separate the central figure from the peripherals and the latter from each other shows that it differs from the condition observed in the southern taxa (in which these structures are "V"-shaped in transversal section). Indeed, in these northern taxa, the transversal section of these sulci has walls parallel to each other and an almost flat bottom. Additionally, the dorsal surface of the osteoderms is always strongly punctate, the osteoderms are thick and the area of articulation between them is notably denticulated.

This notable morphological differentiation between the Patagonian taxa and those from northern South America agrees with the paleobiogeographic scenario outlined by CARLINI et al. (1997) for the middle Miocene. These authors have proposed other possible evolutionary scenarios for the Cingulata at lower latitudes, given the distant phylogenetic relationship between the taxa in both areas, among other elements. The Dasypodidae that are present in northern regions include the Astegotheriinae, Dasypodini, and Tolypeutinae, which are absent in Patagonia; on the contrary, the Peltephilini, Euphractini, and Stegotheriini occur in the latter area (CARLINI et al. 1997). Accordingly, VIZCAÍNO et al. (1990) have suggested a probable intertropical origin for the dasypodine Dasypodidae.

Within the Glyptodontidae, the subfamily Glyptodontinae maintains this primitive pattern of rosette ornamentation ("Araucanian" – Lujanian) (see AMEGHINO 1889; HOFFSTETTER 1958; PASCUAL et al. 1966; PAULA COUTO 1979). In fact, some authors (e.g., CABRERA 1944) have highlighted the notable similarity in dorsal carapace ornamentation between the earliest Glyptodontinae species (*Glyptodontidium tuberifer*; see CABRERA 1944) and the Propalaehoplophorinae. However, in the Glyptodontinae, as in the *Boreostemma* species, the sulci are not parabolic in transversal section, but have parallel sides and a flat bottom ("U"-shaped); this detail has already been noted by authors such as CASTELLANOS (1953) for *Paraglyptodon*. This is coupled to the fact that the dorsal surface of the osteoderms is strongly punctate in the earliest Glyptodontinae (CABRERA 1944; CASTELLANOS 1953), whereas, in the terminal taxa (*Glyptodon* OWEN 1839 and *Glyptotherium* OSBORN 1902), this surface is rugose, with deep and wide sulci (BURMEISTER 1870–1874; AMEGHINO 1889; SOIBELZON et al. 2006; CARLINI et al. 2008).

To sum up, the following trends seem to occur in the glyptodontine Glyptodontidae: **a)** progressive increase of the width and depth of the sulci dividing the central figure from the peripherals; these always with parallel sides and a flat bottom; **b)** increasing rugosity of the dorsal surface of osteoderms, which is openly rugose in the terminal taxa, without secondary peripheral figures; **c)** increasing osteoderm thickness; **d)** tendency of the articulation between osteoderms to become highly denticulated; **e)** lobation of first upper and lower molariforms. The first molariform is already trilobated in *Glyptodon* (see SOIBELZON et al. 2006).

Discussion

The Miocene Glyptodontidae of northern South America (Colombia and Venezuela) have traditionally been included within the Propalaehoplophorinae, and, more precisely, assigned to the genus *Asterostemma*, a taxon originally recognized from Argentinian Patagonia. However, the rosette ornamentation pattern of the dorsal carapace osteoderms (which represented the main basis for these assignations) of southern Propalaehoplophorinae is not the same as that of the northern taxa that were originally assigned to this subfamily. In effect, as we stated, while the sulci shows a "V"-shaped transversal section in the Propalaehoplophorinae and hoplophorine Hoplophorinae, this transversal section is clearly "U"-shaped in the taxa from Colombia and Venezuela. This is coupled to greater complexity of the anterior molariforms, and possession of dorsal osteoderms with extremely punctate dorsal surface, greater thickness, and markedly denticulated articulation surfaces.

This morphologic differentiation between "southern" and "northern" forms agrees with the paleobiogeographic and evolutionary scenario proposed by SCILLATO-YANÉ (1986) and CARLINI et al. (1997) for the cingulate Xenarthra, which was also indirectly anticipated by SIMPSON (1947) and VILLARROEL (1983), given the particular differences observed between most Cingulata from these two areas. As we have previously discussed, in this context, the characters observed in *Asterostemma venezolensis*, *A.? acostae*, and *A. gigantea* justify their exclusion from the genus *Asterostemma* and the Propalaehoplophorinae, and their assignation to our new genus *Boreostemma*. Furthermore, this set of evidences strongly suggests that these taxa represent the first stages in the cladogenesis of the glyptodontine Glyptodontidae.

In agreement with this, the biogeographic and phylogenetic history of the Glyptodontinae was poorly known until now, and it was practically restricted to the southernmost regions of South America. Within this area, their Tertiary records are scarce, relatively late, and show characters typical of the terminal Pleistocene glyptodontines, which suggests that these are already derived taxa.

Thus, the first record of a Glyptodontinae corresponds to *Glyptodontidium tuberifer* from the "Araucanian" (late Miocene – early Pliocene) of NW Argentina (CABRERA 1944). The stratigraphic provenance of this taxon is somewhat uncertain, given that the "Araucanian" is represented by the Andalhuala and Corral Que-

mado formations. However, some datings have suggested that the Andalhuala Fm. could correspond to 7 – 3.54 Ma (BUTTLER et al. 1984; BOSSI et al. 1987; BOSSI & GAVRILOFF 1998; GAVRILOFF 2000; HERRERA & ORTIZ 2005). Likewise, the Corral Quemado Fm. is close to 3.54 Ma in age (BUTTLER et al. 1984); however, datings from the base of this formation range between 4.61 and 4.83 Ma (STRECKER et al. 1989; BOSSI & GAVRILOFF 1998), while the most modern ones correspond to about 2.9 Ma (BOSSI & GAVRILOFF 1998) or are even younger (2.4 Ma?; [sic] BOSSI et al. 1987).

The other Tertiary Glyptodontinae genus is *Paraglyptodon* CASTELLANOS (Pliocene, Chapadmalalan – Marplatan) (see ROVERETO 1914; CASTELLANOS 1953) from South America. One species of this genus (*P. chapalmalensis* AMEGHINO, 1908) is biostratigraphically important, since it is characteristic of the upper Chapadmalan Age/Stage (ca. 3.5 – 3.2 Ma.) (see CIONE & TONNI 2005). Similarly, the distribution of *P. uquiensis* seems to be restricted to the latest Chapadmalalan and the Marplatan (REGUERO et al. 2007).

A remarkable species diversification occurred among the Glyptodontinae during the Pleistocene (ca. 1.8 – 0.008 Ma), along with a wide geographic distribution that was probably stimulated by the expansion of open environments during the glacial periods (CLAPPERTON 1993; CIONE et al. 2003; RABASSA et al. 2005). In fact, these are probably the only Glyptodontidae to successfully partake in the GABI, given that they occur in North America since the early Blancan (ca. 3.9 Ma) (CARRANZA-CASTAÑEDA & MILLER 2004), and evolved several taxa in that subcontinent, from the late Blancan (ca. 2.6 Ma) to the Rancholabrean (late Pleistocene) (GILLETTE & RAY 1981; WHITE & MORGAN 2005; MORGAN & WHITE 2005; CARLINI et al. 2008) (but see DOWNING & WHITE 1995).

To sum up, the evidence indicates that the Mio-Pliocene taxa from Colombia and Venezuela are not Propalaehoplophorinae, but share several derived characters with the glyptodontine Glyptodontidae. Hence it is possible to propose a partial reinterpretation of the phylogenetic and biogeographic history of the Glyptodontinae. Indeed, until the recognition of *Boreostemma* n. gen. in the present contribution, the oldest records of Glyptodontinae (late Miocene – Pliocene) were restricted to southern South America (Buenos Aires, Catamarca and Jujuy provinces, Argentina) and suggested a southern differentiation for the subfamily, probably from advanced Propalaehoplophorinae (CARLINI et al. 1997).

On the contrary, the new evidence presented here strongly suggests that the origin of the Glyptodontinae was geographically located in northern South America and much earlier (middle Miocene) than previously supposed, since the reliable records from the Honda Group, Colombia (*Boreostemma gigantea* and *B. acostae*), date from approximately 13 Ma (CARLINI et al. 1997; KAY et al. 1997).

Suggestively, the first Glyptodontinae records (*Glyptodontidium tuberifer*) in southern South America coincide with what PASCUAL & BONDESIO (1982) called "Age of Southern Plains", which includes the Chasicoan, Huayquerian, Montehermosan, and Chapadmalalan ages (ca. 11 – 3 Ma) (see PASCUAL et al. 1996) and whose beginnings were undoubtedly related to the Quechua Phase of Andean Orogeny (see YRIGOYEN 1979). More precisely, the evidence suggests that the first southern Glyptodontinae records correspond to the latest Miocene or Pliocene, when these great plains reached their maximum development (ORTIZ JAUREGUIZAR 1998), extending from north Patagonia to Venezuela (MARSHALL et al. 1983; ORTIZ JAUREGUIZAR & CLADERA 2006). In fact, some authors have suggested that these climatic-environmental conditions greatly favored the entrance of the first Holarctic immigrants, which already show clear adaptations to open grassland environments (e.g., Cricetidae and Tayassuidae) (VUCETICH 1986; MENEGAZ & ORTIZ JAUREGUIZAR 1995; PARDIÑAS 1995). Thus, it is possible that these great open extensions also favored the dispersion of the glyptodontines into more southern areas through "biogeographical corridors".

The recognition of this new genus and species in northern South America, and the associated systematic and paleobiogeographical consequences, highlight the importance of research in continental sediments at these latitudes, especially considering the proximity to areas that functioned as biogeographic corridors between both American subcontinents (WOODBURNE et al. 2006). These corridors modified the biotic relationships in both Americas, especially in South America, which had almost insular characteristics during a large part of the Cenozoic.

Conclusions

1. The morphological evidence indicates that the propalaehoplophorine Glyptodontidae as previously defined (southern taxa plus taxa from northern South America) are not a natural group.
2. Consequently, we propose the recognition of a new genus (*Boreostemma*) for the Venezuelan and Colombian species previously assigned to *Asterostemma*, while the latter taxon is geographically restricted to Argentina.
3. *Boreostemma* includes the following species: *B. acostae* (VILLARROEL 1983) and *B. gigantea* (CARLINI et al. 1997) from the middle Miocene of La Venta, Colombia, and *B. venezolensis* (SIMPSON 1947) and *B. pliocena* n. sp. from the Miocene and Pliocene of Venezuela, respectively.
4. The characters of this new genus and the species referred to it (e.g., sulci between central and peripheral osteoderms "U"-shaped in transversal section, dorsal surface of osteoderms in the dorsal carapace highly punctate, greater osteoderm thickness, osteoderm articulation highly denticulated and with evident pro-

longations, anterior molariforms complex), suggest the inclusion of these taxa among the glyptodontine Glyptodontidae, which are rare in the fossil record of southern South America for that period.

5. Consequently, it is possible to hypothesize that this genus represents the start of the cladogenesis of glyptodontine Glyptodontidae, which seems to have taken place in much more northern regions than previously supposed. It is also possible that the arrival of these Glyptodontinae to southern South America was favored by the emergence of large open savanna environments during the "Age of Southern Plains".
6. The propalaehoplophorine Glyptodontidae are restricted to the Oligo-Miocene of the southern cone of South America, mainly in Patagonia.

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North American Glyptodontines (Xenarthra, Mammalia) in the Upper Pleistocene of northern South America

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with 4 figures

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Abstract: The Glyptodontidae is one of the most conspicuous groups in the Pleistocene megafauna of the Americas. The Glyptodontinae were involved in the Great American Biotic Interchange (GABI) and their earliest records in North America are about 3.9 Ma, suggesting an earlier formation of the Panamanian landbridge. Taxonomically it is possible to recognize two Pleistocene genera of Glyptodontinae: *Glyptodon* (ca. 1.8 – 0.008 Ma), restricted to South America, and *Glyptotherium* (ca. 2.6 – 0.009 Ma), including records in both North and Central America. Here we present the first report of the genus *Glyptotherium* in South America, from the Late Pleistocene of several fossil localities in Falcón State, northwestern Venezuela. A comparative analysis of the material, represented by cranial and postcranial parts, including the dorsal carapace and caudal rings, suggests a close affinity with *Glyptotherium cylindricum* (Late Pleistocene of Central Mexico). This occurrence in the latest Pleistocene of the northernmost region of South America supports the bidirectional faunal migration during the GABI and the repeated re-immigration from North America of South American clades, as has been reported in other members of the Cingulata (e.g., Pampatheriidae).

Keywords: Glyptodontidae • *Glyptotherium* • Pleistocene • South America • Venezuela • Paleobiogeography • Great American Biotic Interchange

Kurzfassung: Die Glyptodontidae ist eine der auffälligsten Faunengruppen des Pleistozäns Südamerikas. Die Glyptodontinae waren in dem „Great American Biotic Interchange" (GABI) involviert, und ihre frühesten Reste aus Nordamerika sind etwa 3,9 Ma alt, was für eine frühere Entstehung der Panamanischen Landbrücke spricht. Es ist taxonomisch möglich, zwei Genera von pleistozänen Glyptodontinae zu unterscheiden: *Glyptodon* (ca. 1,8–0,008 Ma) aus Südamerika und *Glyptotherium* (ca. 2,6 – 0,009 Ma) aus Nord- und Mittelamerika. Hier stellen wir den ersten Nachweis von *Glyptotherium* in Südamerika, aus dem oberen Pleistozän von verschiedenen Lokalitäten des Bundesstaates Falcón, nordwestliches Venezuela, vor. Eine vergleichende Untersuchung von Schädel- und Postkranialelementen, einschließlich des dorsalen Panzers und kaudaler Ringe, unterstützt eine nahe Verwandtschaft mit *Glyptotherium cylindricum* (Spätes Pleistozän Mittel-Mexikos). Diese spät-pleistozäne Verbreitung im nördlichsten Teil Südamerikas ist ein Nachweis für eine bidirektionale Migration während des GABI und für das Zurückkehren von Taxa von Nordamerika nach Südamerika, wie schon für andere Vertreter der Cingulata (z. B. Pampatheriidae) berichtet wurde.

Schlüsselwörter: Glyptodontidae • *Glyptotherium* • Pleistozän • Südamerika • Venezuela • Paläobiogeographie • Great American Biotic Interchange

Introduction

During the Great American Biotic Interchange (GABI), several taxa of South American mammals, such as Xenarthra and Marsupialia, migrated into North America, while North American taxa such as Cervidae, Felidae, Tapiridae, Ursidae, and Gomphotheriidae migrated into South America, by means of the biological corridor for terrestrial organisms that arose between both continents, first as an island chain and later as an unbroken

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terrestrial connection, starting about 5 Ma (see WEBB 1985, 2006; PASCUAL & WEBB 1989; PASCUAL & ORTIZ-JAUREGUIZAR 1990; TONNI et al. 1992; PASCUAL et al. 1996; WOODBURNE et al. 2006), and ending about 2.7 Ma. The emergence and consolidation of this continuous corridor was strongly influenced by the Pliocene Diaguita phase that triggered the final uplifting of the Panama isthmus, thus allowing and facilitating the definitive biogeographical connection between North and South America (PASCUAL et al. 1996). Recently, CARRANZA-CASTAÑEDA & MILLER (2004) and FLYNN et al. (2005) suggested that this land bridge might have originated more than one million years earlier, but not necessarily continuous in time. This hypothesis is supported by the presence of *Glossotherium*, *Glyptotherium*?, *Plaina* and *Neochoerus* [sic] in central Mexico at approximately 4.7 to 3.6 Ma.

The relationship between both Americas before that time was represented by chains of emerged lands, at least since ca. 9 Ma (SMITH 1985; WEBB 2006). This particular condition undoubtedly exerted strong regulation on both the type and intensity of biotic migrations between these continents, with discretional or specific effects in different cases. Currently it seems evident that the entrance of taxa of Holarctic origin into South America was a more gradual process than previously assumed, given that the biomass and diversity of immigrant taxa appear to be very scarce during the Chapadmalalan and Marplatan (ca. 3.9 – 1.8 Ma) (TONNI et al. 1992; CIONE & TONNI 2001) and become more evident during the Ensenadan – Lujanian (ca. 1.8 – 0.008 Ma (CIONE & TONNI 1995a, b, 2005). In North America, the first reliable records of South American immigrants correspond to the Hemphillian (ca. 9 Ma, WEBB 2006); subsequently these records occur continuously from the late Blancan (ca. 2.7 Ma) in southwestern USA (WOODBURNE & SWISHER 1995; MORGAN & WHITE 2005; WHITE & MORGAN 2005; WEBB 2006).

The Xenarthra are one of the groups of South American mammals that were actively involved in the faunal exchange, given that both the Phyllophaga (Megatheriidae, Megalonychidae and Mylodontidae) and the Cingulata (Dasypodidae, Pampatheriidae and Glyptodontidae) reached North America, and even differentiated into new taxa characteristic of the latter continent. Among the Cingulata, the glyptodontine Glyptodontidae entered North America during the early Pliocene (middle Blancan; ca. 3.9 Ma; CARRANZA-CASTAÑEDA & MILLER 2004; WHITE & MORGAN 2005; MORGAN & WHITE 2005; FLYNN et al. 2005), with the subsequent differentiation of a genus different from the South American *Glyptodon* OWEN (see GILLETTE & RAY 1981).

Unlike the South American Glyptodontinae, for which no recent revision is available (SOIBELZON et al. 2006), the North American taxa were studied by GILLETTE & RAY (1981). These authors concluded that only one genus can be recognized; based on priority, this is *Glyptotherium* OSBORN (= *Brachyostracon* BROWN = *Boreostracon* SIMPSON = *Xenoglyptodon* MEADE), with a temporal distribution that ranges from the Pliocene to the late Pleistocene. In this taxonomic context, CARRANZA-CASTAÑEDA & MILLER (2004) have reported some isolated scutes from central Mexico that they referred to ?*Glyptotherium*, coming from sediments dated at ca. 3.9 Ma. This genus, with certainty present in North America since ca. 2.6 Ma, diversified into five described species: **a)** *G. texanum* OSBORN (late Blancan; late Pliocene), distributed in the southern US; **b)** *G. arizonae* GIDLEY (late Blancan – early Irvingtonian; late Pliocene – early Pleistocene), with unquestionable records in the southern US; **c)** *G. floridanum* (SIMPSON) (Rancholabrean; late Pleistocene), with numerous records in central-south and southeastern US, and central and central-south Mexico; **d)** *G. mexicanum* (CUATÁPARO & RAMÍREZ) (late Rancholabrean; late Pleistocene), known only from the holotype, from central-south Mexico; and **e)** *G. cylindricum* (BROWN) (early Rancholabrean; late Pleistocene), which like the previous case is known only from the holotype, found in central-western Mexico (GILLETTE & RAY 1981).

The presence of *Glyptotherium* in Central America has been mentioned by WEBB & PERRIGO (1984) for the late Pleistocene of Panama and Honduras, and by CISNEROS et al. (2001) and CISNEROS (2005) for the Pleistocene (Irvingtonian?) of El Salvador.

Until now, all the records of glyptodontine Glyptodontidae from Venezuela have traditionally been referred to the genus *Glyptodon* (a.o., KARSTEN 1886; ROYO GÓMEZ 1960; CRUXENT 1967; CASAMIQUELA 1979; BOCQUENTIN VILLANUEVA 1982a, b; OCHSENIUS 1980; AGUILERA 2006), primarily on the basis of dorsal carapace osteoderms recovered from upper Pleistocene fossil beds. These remains have been alternately designated as *Glyptodon clavipes* (ROYO GÓMEZ 1960; OCHSENIUS 1980), *G.* cf. *clavipes* and cf. *Glyptodon* (CASAMIQUELA 1979; AGUILERA 2006), with variable degrees of certainty and mostly without comparative anatomical analyses to support these assignments.

A detailed study of these materials from the uppermost Pleistocene, including skulls, postcranial skeletons, dorsal carapaces and caudal rings, especially from the localities TaimaTaima, Muaco, Cucuruchú, and Quebrada Ocando in Falcón State, Venezuela (Fig. 1), indicates that all of them are in fact assignable to the genus *Glyptotherium* and morphologically similar to *G. cylindricum*. Consequently, this represents the first record of this North American glyptodontine genus for South America, considerably expanding its geographic distribution to 70° W.

Even though the GABI has usually been interpreted as unidirectional migrations between both Americas through the Panama landbridge, some cases of re-entrance have been verified. Indeed, SCILLATO-YANÉ et al. (2005) recently addressed the emigration of pampatheriid Cingulata toward North America during the

Fig. 1. Location map, showing main localities where *Glyptotherium* cf. *cylindricum* was identified among fossil remains.

late Pliocene, the latter differentiation of a new genus in North America, and its subsequent re-entrance into South America during the Pleistocene, simultaneous with a second emigration of Pampatheriidae. Within this dynamic biogeographic scenario, the presence of *Glyptotherium* cf. *G. cylindricum,* in the upper Pleistocene of the extreme northern South America is probably the second example among Xenarthra of re-entrance of fauna of South American origin that differentiated in North America and then re-entered the southern subcontinent.

This paper deals mainly with the paleobiogeography of Late Pleistocene North American Glyptodontinae, including one species, *Glyptotherium* cf. *cylindricum* BROWN, 1912, that reached South America at some time during the latest Pleistocene. We also provide support for the generic differences between *Glyptotherium* and *Glyptodon*, and provide some considerations about climate and other environmental factors that may have influenced their differentiation and their time of dispersal into South America.

Abbreviations used in the text: AMNH, American Museum of Natural History, New York, USA; GABI, Great American Biotic Interchange; M, m, upper and lower molariform respectively; MCN, Museo de Ciencias de Caracas, Venezuela; n/n, without official catalog number; UCV, Universidad Central de Venezuela, Caracas, Venezuela; UNEFM-CIAAP, Universidad Nacional Experimental Francisco Miranda, Coro, Venezuela - Centro de Investigaciones Antropológicas, Arqueológicas y Paleontológicas.

Systematic paleontology

Xenarthra COPE, 1889
Cingulata ILLIGER, 1811
Glyptodontoidea GRAY, 1869
Glyptodontidae GRAY, 1869
Glyptodontinae GRAY, 1869
Glyptotherium OSBORN, 1903

Glyptotherium cylindricum (BROWN, 1912) sensu GILLETTE & RAY, 1981

Syn. *Brachyostracon cylindricum* BROWN, 1912

Holotype: AMNH 15548, hyoid, skull fragment, atlas, fragments of ribs, 20 isolated molariforms, complete dorsal carapace and fragments of caudal rings.
Type locality and age: Area near Ameca (105° W), Jalisco, Mexico (BROWN 1912); late Pleistocene sediments (see GILLETTE & RAY 1981).

Glyptotherium cf. *cylindricum* (BROWN, 1912) sensu GILLETTE & RAY, 1981

Figs. 2–3

Description and assignation of material

Skull: The skull (MCN n/n) of *Glyptotherium* cf. *cylindricum* from Venezuela (Figs. 2A–D) is generally similar to that of *Glyptotherium texanum*, *Glyptotherium floridanum* and *Glyptotherium arizonae*. It is clearly distinguished from *Glyptodon munizi*, *Glyptodon clavipes* and *Glyptodon reticulatus* by its greater anteroposterior elongation, greater postorbital and bizygomatic diameter, evident forward prolongation of the predental portion of the palate, and less upward inclination of the dorsal skull profile, particularly in the parieto-occipital region in lateral view.

In lateral view, the angle formed by the palatal plane and the dorsal skull profile in *G.* cf. *cylindricum* is much more open than in *G. munizi* and *G. clavipes*, forming an angle similar to the one in *Glyptotherium texanum* and *G. floridanum*. Consequently, the dorsal profile of *G.* cf. *cylindricum* is more inclined upwards and backwards than in *G. munizi*, and much more than in *G. clavipes*; the nasal bones are almost at the same level as the dorsal portion of the frontals and parietals. The development of the entire occipital region is similar to that of the other *Glyptotherium* species, but much less than that of *Glyptodon*. The anteroposterior development of the squamosal portion of the zygomatic arch is greater than in *G. clavipes* and similar to that of *G. munizi*, as one of the main consequences of the greater skull elongation. The anteroposterior diameter of the orbital notch is greater than its dorsoventral diameter. This differentiates this species from *G. arizonae*, whose orbital notch has greater dorsoventral diameter and subelliptical outline. Likewise, the orbital notch of *G. munizi*, *G. clavipes* and *G. reticulatus* is almost completely circular and its anteroinferior border, formed by the uppermost part of the descending process of the maxilla and jugal, has a thickened rim that is not present in *G.* cf. *cylindricum*, *G. arizonae* or *G. floridanum*. Posteriorly, the orbit is freely communicated with the temporal fossa, as in *Glyptodon* and the Hoplophorinae, and differing from *Doedicurus*, in which the orbit is closed posteriorly. Anteriorly, the area comprising the alveolar portion of the maxillae is more extended anteroposteriorly than in *Glyptodon*, very similar to the condition observed in *G. arizonae*, *G. texanum* and *G. floridanum*. This greater rostral elongation is particularly evident in the predental portion of the palate that extends forward greatly in advance of the nostrils as in *G. floridanum*, and contrasting with *Glyptodon*, in which the premaxillae, maxillae, nasals, and frontals end at the same level, forming a vertical plane. As is characteristic of Pleistocene glyptodontines, the nasals and premaxillae are considerably reduced (LYDEKKER 1894; BURMEISTER 1864; SOIBELZON et al. 2006).

In frontal view, the nostrils are heart-shaped, with the upper margin wider than the lower one; they are somewhat similar to those of *G. arizonae*, and the Hoplophorinae *Eosclerocalyptus proximus* and *Plohophorus figuratus*. In *Glyptodon clavipes* and *G. munizi* these openings are clearly subtriangular, with free margins of the maxillae straight and more developed septum that separates both nasal cavities. The infraorbital foramina are at the same level as in the remaining *Glyptotherium* species, and show no significant differences. The orientation of the exiting infraorbital foramina is clearly anterior, as in *G. clavipes*, and differing from the condition of *G. munizi*, in which the opening of this foramen is rather laterally oriented. The descending processes of the maxillae are markedly divergent ventrally, and their internal margins are almost completely straight, as in *G. arizonae*. This particular morphology distinguishes this taxon from the genus *Glyptodon*, in which the descending processes of the maxillae are generally curved toward the sagittal plane, so that their internal margins are clearly concave.

Dorsally, the nuchal ridges at both sides of the supraoccipital are widely open, forming an angle of about 180° with each other, whereas this angle is more closed, about 120°, in *G. clavipes* and *G. munizi*. These ridges do not form a defined sagittal ridge on the parietals near or at the skull midline, as in *G. reticulatus*, *G. munizi* and *G. clavipes*. As in all Glyptodontidae, this area presents numerous vascular and nervous foramina largely concentrated on the parietals, which are small and restricted to the dorsal region of the skull. The absence of a sagittal crest is also observable in *G. arizonae*. Anteriorly, the entire area demarcated by the supraoccipital ridge and the postorbital apophyses of the frontal bone is noticeably more expanded transversally than in *G. clavipes*, and much more so than in *G. munizi*; the condition in this taxon is very similar to that of *G. arizonae* and *G. texanum*. This greater widening is especially evident at the level of the postorbital narrowing. The zygomatic arches form a semicircle more evi-

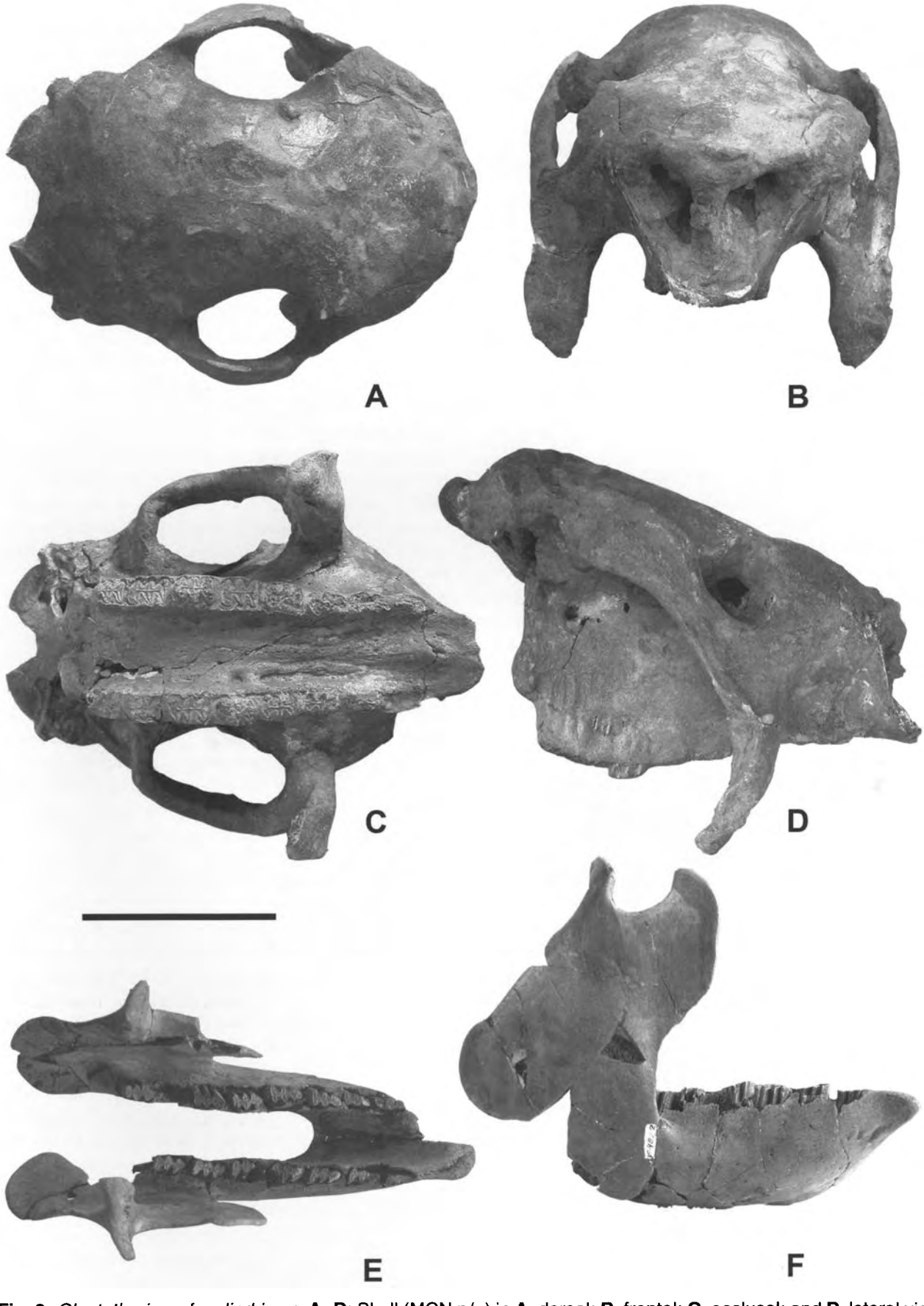

Fig. 2. *Glyptotherium* cf. *cylindricum*. **A–D**: Skull (MCN n/n) in **A**. dorsal; **B**. frontal; **C**. occlusal; and **D**. lateral view. **E–F**: Mandible (UCV n/n) in **E**. occlusal; and **F**. lateral view. – Scale bar = 10 cm.

dent than in *Glyptodon*, in which they tend to be straighter. The surface formed by the frontal bones is distinctly convex anteriorly to the postorbital apophyses, so that its lateral margins are also somewhat convex. This area is clearly different from that of *G. munizi*, *G. reticulatus* and *G. clavipes*, because it is nearly flat, and consequently presents straight lateral margins. This entire area is largely subtriangular in *Glyptodon*, with the apex directed toward the mid-distal end of the nasals.

The foramen magnum is oval, with its long axis transversal. In occlusal view, the palate is wide and the premaxillae are less shortened than in *Glyptodon*, similar to the other *Glyptotherium* species. Both molariform series are more separated posteriorly; this condition is especially evident at the level of M4. The predental portion of the palate, formed by the maxillae and premaxillae, is markedly extended anteroposteriorly, very similar to that of *G. floridanum* and the Hoplophorinae *Eosclerocalyptus proximus*, in which this area is subtriangular. This condition differs remarkably from that of *Glyptodon*, in which this zone is truncated and subquadrangular. Four or five large foramina open at both sides of the dental series, at the level of molariforms M4–M6. The infraorbital foramina are at the level of a plane projecting between M2 and M3, and the ventralmost point of the descending process of the maxilla coincides with a plane passing through the first lobe of M4, as in *G. arizonae* and *G. texanum*. In the posterior palate region, immediately behind M8, the small palatine bones are restricted to the lower margin of the choanal opening.

Dentition: All the upper and lower molariforms are lobed and with secondary osteodentine ramifications (Figs. 2C, E); the latter is probably a synapomorphy of Glyptodontinae. The m1 of *G. cylindricum* is characterized by its clear trilobation, even more marked than in the remaining *Glyptotherium* species, with well developed notches separating the lobes, particularly on the labial side. This differentiates this species from *G. munizi*, in which the lobation is almost nonexistent on the lingual side, and from *G. floridanum*, in which m1 is simple and ovoid in transverse section. In *G. cylindricum*, bilateral development of the last lobe of m1 is asymmetric, so that the lobe is more evident labially than lingually. The morphology of m2 and m3 is similar to that of m1, only larger, and with the third lobe showing more asymmetric bilateral development; these teeth are somewhat similar to those of *G. munizi, G. clavipes, G. arizonae*, and the m3 of *G. floridanum*. From m4 to m8, all molariforms have the same basic morphological pattern, whereas the last lobe is inclined approximately 80° degrees with respect to the sagittal plane; this condition clearly differentiates this taxon from *Glyptodon*, in which the transverse axis of the last lobe forms a 90° angle with respect to that plane. Lastly, the third lobe is markedly smaller, as in *G. floridanum*. Generally, the lower dentition of *G.* cf. *cylindricum* is similar to that of *G. arizonae*, but can be differentiated from this taxon by presenting a less asymmetrical bilateral development, particularly in molariforms m1–m5.

M1 is lobed, although the notches separating the lobes are poorly developed, and the transverse axis of the first lobe is inclined 50° with respect to the anteroposterior axis of the dental series. M2 is evidently trilobated; the occlusal surface of its first lobe is much more expanded labially and presents the same inclination observed in M1. The next two molariforms (M2 and M3) are similar, except that the first lobe progressively loses the original inclination and the posterior margin of the last lobe acquires a convex outline. Molariforms M4 to M8 are similar to each other; they are characterized by symmetrical bilateral development of the first lobe and by having the transverse axis perpendicular to the longitudinal axis of the dental series. In these teeth, the anterior margin of the first lobe is almost completely flat, except for M8, in which this anterior margin is slightly concave. A particular feature of *G.* cf. *cylindricum* occurs in the last lobe of these molariforms, in which the lingual half, more expanded than the labial half, presents a very convex internal margin; numerous secondary ramifications of vasculodentine appear in this lingual half. This is also observable in *G. arizonae*, but the reduction of the labial half of the molariform is more marked in the latter species.

Mandible: The mandible of *G.* cf. *cylindricum* (UCV n/n) is slender (Figs. 2E, F) and morphologically similar to that of *G. texanum* and *G. floridanum*. It differs clearly from that of *Glyptodon* and *Glyptotherium arizonae* by the much greater robustness in the latter taxa. In lateral view, the horizontal ramus is lower than in *Glyptodon* and *Glyptotherium arizonae*, and its inferior margin is slightly convex, almost straight, and parallel to the molariform series as in *G. floridanum* and *G. texanum*. This particular morphology distinguishes this taxon from the genus *Glyptodon* and from *G. arizonae*, in which the horizontal ramus is very deep, with a markedly convex ventral margin. Anterior to the m1, the predental portion of the symphyseal region is at a level with the molariform series along its entire anteroposterior extension, and consequently its dorsal margin is horizontal and straight, whereas in *Glyptodon* the distalmost third of this structure tends to incline downwards, so that its dorsal margin is somewhat convex. Likewise, this region is more extended longitudinally than in *Glyptodon*. The symphyseal region is shorter than in *G. munizi*, *G. clavipes* and *Glyptotherium arizonae*. Posteriorly, this region ends at approximately a vertical plane passing through the first lobe of m4, as in *Glyptodon* and the remaining *Glyptotherium* species. The ascending ramus is remarkably tall and wide at the alveolar level; it begins at the level of the first lobe of m6, rising at an angle of about 60° to 70° with respect to the occlusal plane. Its anterosuperiormost point coincides with

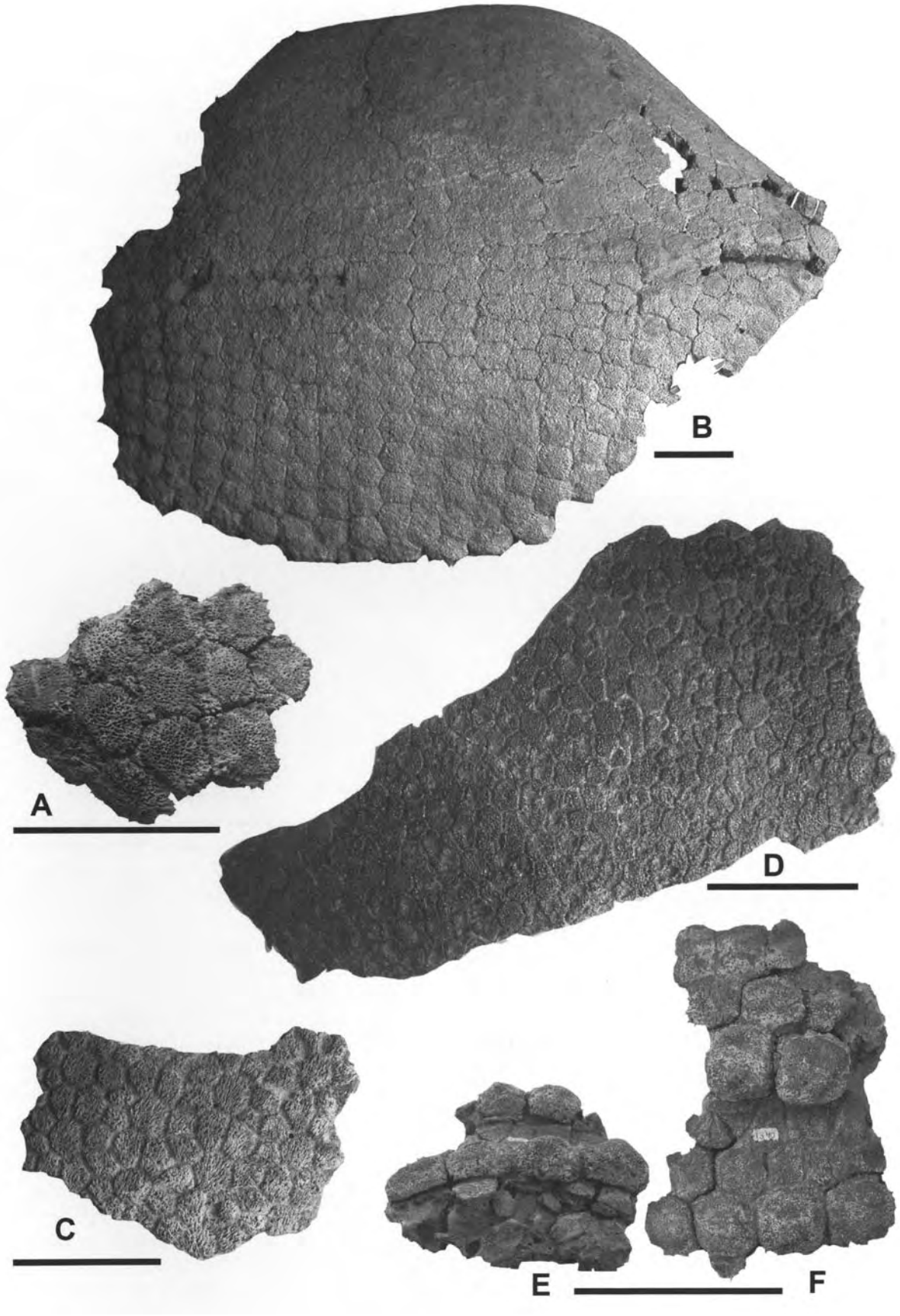

Fig. 3. *Glyptotherium* cf. *cylindricum*. **A**: (CIAAP n/n) articulated osteoderms of a partial cephalic shield in dorsal view (anterior to left). **B**: (CIAAP n/n) articulated osteoderms of a partial caparace in left lateral view. **C–D**: (MCN n/n) aticulated osteoderms of a partial caparace of one specimen, showing the rugose external surface. **E–F**: (UNEFM 1540) articulated osteoderms of two partial caudal rings, each of them formed by three osteoderm rows; E. posterior and F. external view. – Scale bar = 10 cm.

the projection of the m5-m6 boundary. The lower half of the anterior margin of the ascending ramus bears a very marked notch delimiting a clearly concave region at the level of the molariforms. This concavity is much less marked in *Glyptodon*, *G. arizonae* and *G. floridanum*.

Cephalic shield: The preserved fragment of a cephalic shield (UNEFM-CIAAP n/n) consists of twelve articulated osteoderms (Fig. 3A). The ornamentation of these osteoderms is similar to that of the carapace, only less evident, and the central figure of each osteoderm is somewhat raised with respect to the peripheral figures. Each osteoderm has a central subcircular figure with an extremely rugose dorsal surface and numerous perforations that increase its rugosity. Each central figure is surrounded by a row of poorly developed small peripheral figures. The morphology of these osteoderms is very different from that of *Glyptodon*, in which most of the cephalic shield is formed by small polygonal osteoderms presenting a smoothly convex dorsal surface with no signs of ornamentation (SOIBELZON et al. 2006: 382).

Carapace: A large articulated portion of the posterolateral region is preserved (UNEFM-CIAAP 578) (Fig. 3B). The dorsal profile is markedly convex in lateral view, as in *Glyptotherium cylindricum* (AMNH 15548), and somewhat similar to that of the Propalaehoplophorinae *Propalaehoplophorus* and *Cochlops*. This characteristic morphology differentiates this taxon from *Glyptodon clavipes* and *G. munizi* that have carapaces with greater anteroposterior diameters and less convex dorsal profiles. The region adjacent to the caudal notch is clearly inclined upwards, as described for *Glyptotherium cylindricum* (GILLETTE & RAY 1981: 184). This character is absent in *Glyptotherium texanum*, but present in *Glyptotherium arizonae*, although the condition is less marked in the latter species. The osteoderms are characterized by a primitive ornamentation pattern, consisting of a circular or subcircular central figure encircled by a row of polygonal peripheral figures, which are always smaller than the central one, as in *Glyptodon*. However, in contrast with the condition in *Glyptodon*, in which the exposed surface is almost smooth (AMEGHINO 1889; SOIBELZON et al. 2006), in *Glyptotherium* the exposed surface is extremely rugose (Figs. 3C, D), with numerous perforations, and the peripheral figures are less symmetrical in some osteoderms. In some portions of the carapace the perforations are more evident and present distinct oblique dorso-ventral orientation.

Caudal rings: Fragments of two associated caudal rings from a region close to the caudal notch are preserved (UNEFM 1540) (Figs. 3E, F). Each ring is formed by three transverse rows of osteoderms, in contrast with *G. munizi, G. clavipes, G. texanum, G. floridanum*, and *G. arizonae* in which there are only two rows of osteoderms. Each distalmost row is formed by quadrangular osteoderms with clearly convex, very rugose and punctuated exposed surfaces. A small conical prominence occurs at the middle of the posterior margin of each osteoderm, which is morphologically very similar to that of *G. floridanum* and *G. arizonae*, and clearly different from that of *Glyptodon*. In the latter taxon these tubercles are generally much more developed, forming pointed conical structures, similar to bony "spines". The middle row is formed by smaller osteoderms, mostly hexagonal and with a flat or slightly convex dorsal surface, but never as convex as the osteoderms in the distalmost row. The proximalmost row comprises pentagonal osteoderms with the same morphology as that described above, but with plainly flat exposed surfaces. The proximal third of each osteoderm is noticeably thinner, flat and rectangular, representing the articulation with the preceding caudal ring.

Provenance of material

Most of the material studied comes from archaeological sites containing megafauna, or from latest Pleistocene palaeontological sites. Notwithstanding, in 2006 we found a complete carapace in the northern town of Urumaco, and one of us (OA) saw isolated broken osteoderms in the Paraguaná Peninsula (Fig. 1). Outside Estado Falcón, some other sites (e.g., Lago de Valencia, Maracay, Estado Aragua, A. Jaimes pers. com.) might have *G.* cf. *cylindricum* among its faunal assemblages, but we have not yet studied the remains.

TaimaTaima: This site is 2.5 km northwest of TaraTara, Colina Municipality, Falcón State, in an area with "ojos de agua" or ascending spring waters (11° 29' 57" N and 69° 31' 18" W). The Pleistocene sediments consist of gray clayey sands arranged in a layer 0.75 to 1 m thick, overlying a pavement formed by coquinoid sandstone that belongs to the TaimaTaima Member of the Caujarao Formation (upper Miocene). The TaimaTaima fossil bed was described and studied by BRYAN (1979) and GRUHN & BRYAN (1984), and divided into four units, of which Unit I has the greatest palaeontological significance. The superficial portion of this Unit I, above the current phreatic level, is oxidized, and the lower third was saturated with water at the time of excavation. The top of Unit I is conspicuous due to an evident unconformity that indicates an erosional episode. The remaining paleosoil, with a layer of pebbles and abundant fragmentary fossils, overlies the unconformity. The paleofaunal association at the unconformity between Units I/II forms the third faunal horizon that represents the last evidence of megafauna at the TaimaTaima site. The reddish sands that underlie Unit II are barren. The uppermost stratigraphic unit is a stratum of brown sands, also barren. The age of the fossil-bearing unit (Unit I) was established on the basis of radiocarbon (C^{14}) dating of diverse types of samples: TAMERS (1971)

dated bones and sediment samples, obtaining an age between 14,000 and 12,000 radiocarbon years BP; similarly, GRUHN & BRYAN (1984), based on the analysis of plant remains, dated it at between 12,580 ± 150 and 13,390 ± 130 radiocarbon years BP.

Muaco: This site is in the Muaco village, between the Muaco harbour and Carrizal, Colina Municipality, Falcón State, precisely at the location of "ojos de agua" or ascending spring waters (11° 28' 51"N and 69° 32' 41"W). The site consists of a layer of Pleistocene muddy sediments, 2 to 3 m thick, overlying Miocene sandstones that belong to the Caujarao Formation. The fossils were found sunk in the mud, above the sandstone (ROYO GÓMEZ 1960). The age of the fossil-bearing unit has been established at between 14,300 ± 500 and 16,375 ± 400 radiocarbon years before present (OCHSENIUS 1980; ROYO GÓMEZ 1960; ROUSE & CRUXENT 1963).

Cucuruchú: This is located at a low hill near Cucuruchú creek, which drains into the Agua Divina gully, between Curazaito and TaimaTaima, in Colina Municipality, Falcón State, about 200 m away from the coast line (11° 30' 10"N and 69° 30' 17"W). There are several ascending springs around the fossil deposit area. The site consists of a thin layer of fragments of rounded limestone rocks ranging in size from pebbles to cobbles and embedded in a clayey matrix. This layer of fluvial Pleistocene sediments is between a few centimetres and half a metre thick, and it is the main fossil-bearing layer. Above the pebble level there is a massive gray to brown clayey layer with impressions of stems and leaves. Its current thickness is 10 m but it was probably thicker originally, and is very probably lacustrine in origin. Some fragmentary fossil remains have been found in the lower section of these clays (CRUXENT 1970). The age of the fossil-bearing unit could not be dated reliably, and the results obtained by BRYAN (1973) correspond in all probability to rejuvenated samples (5,860 ± 80 radiocarbon years BP). This age is not consistent with the late Pleistocene faunal association found in this fossil bed.

Quebrada Ocando: This bed is located in the valley formed by the Quebrada Ocando southeast from the Mataruca hamlet, in Colina Municipality, Falcón State (11° 25' 08"N and 69° 29' 47"W). The site consists of a layer of rounded limestone fragments ranging in size from pebbles to cobbles, in a matrix of pale yellow Pleistocene clayey sands; it is 1 to 3 m thick and is the main fossil-bearing layer. No information about the age of the fossil-bearing unit is available.

Discussion

The phylogenetic history of the Glyptodontinae is peculiar and poorly known at present. The earliest record is represented by *Glyptodontidium tuberifer* CABRERA, 1944, from the "Araucanian" (late Miocene – early Pliocene; ca. 8.7 – 3.9 Ma) of Catamarca and Tucumán provinces, Argentina. Another, poorly characterized genus included in this subfamily is *Paraglyptodon* CASTELLANOS, 1932, from the Pliocene of Argentina; one of the species of this genus (*P. chapadmalensis* AMEGHINO, 1908) is of biostratigraphical importance as characteristic of the upper Chapadmalalan Stage/Age (ca. 3.5 – 3.2 Ma) (see CIONE & TONNI 1995b, 2005). Another species recognized is *P. uquiensis* CASTELLANOS (Marplatan; ca. 3.2 – 1.8 Ma), which partly resembles the Pleistocene genus *Glyptodon*, particularly in skull features (CASTELLANOS 1953).

Although this subfamily has not yet been subject to cladistic analysis, the Glyptodontinae clearly appear to be a natural group. In this sense, the main synapomorphies that support the monophyly of this taxon are the conical osteoderms forming the margins of the carapace, and the presence of secondary hard dentine ramifications in the molariform teeth (SCILLATO-YANÉ et al. 1995; CARLINI & SCILLATO-YANÉ 1999). Additional characters include a very constant, rosette-shaped ornamentation pattern and a very solid and thick carapace (see HOFFSTETTER 1958; PAULA COUTO 1979). Likewise, the phylogenetic relationships between Glyptodontinae and the other glyptodontid subfamilies (Propalaehoplohorinae, Glyptatelinae, Hoplophorinae, and Doedicurinae) remain uncertain, although some preliminary phylogenetic analyses tentatively place the Glyptodontinae as sister group of the Doedicurinae (see FERNÍCOLA et al. 2002; FERNÍCOLA 2005).

According to BOMBIN (1976), FIDALGO & TONNI (1983), UBILLA (1985), SCILLATO-YANÉ et al. (1995), and FARIÑA (1996), the Glyptodontinae seems to have evolved in open habitats with grasslands and steppes. In addition, recent analyses of the hyoid apparatus of *Glyptodon* (PÉREZ et al. 2000) and the remarkable hypsodonty attained by these Cingulata (FARIÑA & VIZCAÍNO 2001) suggest a primarily grazing diet.

Already in the early Pleistocene (ca. 1.8 Ma), *Glyptodon* (the only Glyptodontinae) was one of the most conspicuous taxa within the South American "megafauna", considering the notable frequency of discoveries referable to this subfamily. From a stratigraphical viewpoint, the oldest well-characterized species is *Glyptodon munizi*, from the Ensenadan of the localities Mar del Plata and the "Toscas" of Rio de La Plata, Buenos Aires province, Argentina (SOIBELZON et al. 2006). According to available magnetostratigraphical information, the sedimentary sequence of the "Toscas" of Río de La Plata ranges between 1.7 and 0.98 Ma (early – middle Ensenadan) (BIDEGAIN 1991). This taxon is morphologically very similar to the most derived species of the genus (*G. clavipes* and *G. reticulatus;* see DUARTE 1997; SCILLATO-YANÉ et al. 1995; CARLINI & SCILLATO-YANÉ 1999), although distinguished by less lobation of the first molariform, greater skull elongation and narrowing of the region between the postorbital apophysis and supraoccipital ridge (see SOIBELZON et al. 2006).

From a biogeographic viewpoint, *Glyptodon* (Ensenadan – Lujanian) is the genus with the greatest latitudinal range among the Glyptodontidae, with remains found in Argentina (see AMEGHINO 1889; CARLINI & SCILLATO-YANÉ 1999, among others), Paraguay (HOFFSTETTER 1978; CARLINI & TONNI 2000), Uruguay (UBILLA 1996; UBILLA & PEREA 1999; UBILLA et al. 2004), Brasil (see BOMBIN 1976; OLIVEIRA 1999; RANZI 2000, among others), Bolivia (OPPENHEIM 1943; TAKAI et al. 1984; MARSHALL & SEMPERE 1991; WERDELIN 1991), Peru (PUJOS & SALAS 2004), Ecuador (MARSHALL et al. 1984), and probably Colombia (BOMBIN 1981). Within South America, *Glyptodon* is scarce in the Amazonian region (see RANZI 2000), but relatively frequent in coastal and Andean regions (PUJOS & SALAS 2004). Its presence in Central America, especially in Mexico, is uncertain and in need of revision (PAULA COUTO 1979; GILLETTE & RAY 1981). However, outside of the current Argentine territory, most of the records are only identified to genus level and require urgent revision considering their remarkable latitudinal range (see MARSHALL et al. 1984; UBILLA & PEREA 1999; OLIVEIRA 1999; PUJOS & SALAS 2004; UBILLA et al. 2004).

In this sense, the Glyptodontinae is probably the only member of the family that participated in the GABI (GILLETTE & RAY 1981) and then had a cladogenesis in North America that is represented by several species. The earliest records of Glyptodontinae in North America are ca. 3.9 Ma, from the state of Guanajuato in central Mexico (CARRANZA-CASTAÑEDA & MILLER 2004; FLYNN et al. 2005). Notwithstanding, it is possible that another subfamily also participated, the Glyptatelinae, only represented by *Pachyarmatherium leiseyi* DOWING & WHITE, 1995, which was originally described as a Dasypodidae.

In North America, the only recognized glyptodontine genus is *Glyptotherium* (Early Pliocene? – Late Pliocene – Late Pleistocene), with a latitudinal distribution ranging from approximately 37° N to probably 13–14° N (GILLETTE & RAY 1981; WEBB & PERRIGO 1984; CZAPLEWSKI 2004). Until the present, all the records with clear species-level identification are restricted to the southern US and Mexico.

From a stratigraphic perspective, the earliest unquestionable record for the genus is represented by *Glyptotherium texanum*, collected from the 111 Ranch locality (Arizona, US), from sediments dated at approximately 2.6 Ma, immediately below the Gauss/Matuyama boundary, and which probably represents the first stages of the migration of these taxa from South to North America (ca. 2.7 Ma; WHITE & MORGAN 2005; MORGAN & WHITE 2005; WEBB 2006; but see CARRANZA-CASTAÑEDA & MILLER 2004; FLYNN et al.. 2005). The most recent records correspond to *Glyptotherium floridanum*, whose biochron coincides with the Rancholabrean age (ca. 0.3 – 0.009 Ma) (MORGAN & HULBERT 1995).

In Central America, *Glyptotherium arizonae* has been reported for the early Pleistocene (early – middle?; Irvingtonian?) of El Salvador (CISNEROS et al. 2001; CISNEROS 2005); however, species identification is still provisional, as the materials comprise isolated osteoderms and three molariforms and have been classified partly on the basis of stratigraphical criteria. WEBB & PERRIGO (1984) cited the presence of *Glyptotherium* sp. in the late Pleistocene of Honduras and Panamá, and JACKSON & FERNANDEZ (2005) identified *G. floridanum* from Honduras, which thus represents the southernmost record for Central America.

Of the five species recognized as valid by GILLETTE & RAY (1981), *G. cylindricum* is, together with *G. floridanum* and *G. mexicanum*, one of the species occurring in younger sediments, considering that all are restricted to the Rancholabrean (late Pleistocene).

From an anatomical viewpoint, the more derived species of the genus (*G. mexicanum*, *G. floridanum* and *G. cylindricum*) are clearly differentiated from those with earlier records (*G. texanum* and *G. arizonae*) by the following characteristics: a) *G. cylindricum* (AMNH 15548) and *G. mexicanum* show evident shortening of the dorsal carapace, whereas the dorsal profile becomes very convex in lateral view and the area adjacent to the caudal notch is inclined upwards; b) in *G. floridanum* (USNM 6071) the rostral area is elongated anteroposteriorly; this morphology becomes quite evident at the prolongation of the predental portion of the palate; c) the angle formed by the palatal plane and the dorsal profile of the skull is less acute (ca. 35°); d) the mandible is more gracile, differing from that of *G. arizonae*, which is morphologically more similar to the species of *Glyptodon*.

In this context, the remains found in the late Pleistocene of Venezuela, in the localities TaimaTaima, Muaco, Cucuruchú, and Quebrada Ocando, in Falcón State (and which were originally assigned to *Glyptodon*), clearly correspond to genus *Glyptotherium*, and thus represent the first record for this genus in South America, thus considerably expanding its distribution to 70° W and 11° N. This genus assignment is based on the following: a) dorsal surface of the dorsal carapace osteoderms very rugose, different from those of *Glyptodon*, in which they are smoother (see DUARTE 1997; TONNI & BERMAN 1988; RINDERKNECHT 2000); b) absence of the typical bony "spines" observed in the caudal rings of *Glyptodon* (see AMEGHINO 1889; SOIBELZON et al. 2006); c) more gracile mandibular horizontal ramus, with predental symphyseal region markedly prolonged anteroposteriorly, and molariform series (particularly m1–m3) morphologically more primitive; d) ventral margin of horizontal ramus subparallel to the molariform series; d) skull markedly elongated anteroposteriorly, and with greater postorbital and bizygomatic diameters; e) rostral area remarkably prolonged forward, particularly the predental portion of the palate.

On the other hand, the species assignment is somewhat uncertain due to the relatively poor knowledge of *G. cylindricum*, which is limited to the holotype, the most significant element of which is a dorsal carapace in excellent condition (AMNH 15548). This specimen is characterized by its notable anteroposterior shortening, markedly convex dorsal profile and upward curvature of the region adjacent to the caudal notch (BROWN 1912; GILLETTE & RAY 1981). One carapace from Taima Taima examined – UNEFM-CIAAP 578 – (Fig. 3B) shows remarkable similarities to that of the type of *Glyptotherium cylindricum* (see GILLETTE & RAY 1981: fig. 87). Likewise, the upper molariform series corresponding to specimens from Venezuela are morphologically very similar to those figured by GILLETTE & RAY (1981: 60) as belonging to *G. cylindricum*. With respect to the skull, the notable elongation of the rostral area, similar to the condition in Late Pleistocene *Glyptotherium* species, is evident.

From a biogeographic perspective, the distribution of *Glyptotherium* supports the hypothesis of rapid entrance and dispersion of Glyptodontinae into North America during the GABI, given that the earliest unquestionable records referred with certainty to this genus (but see CARRANZA-CASTAÑEDA & MILLER 2004; FLYNN et al. 2005) are ca. 2.6 Ma old (*G. texanum*), coincident with the first evidence (or shortly after) of massive immigration from South America after the formation of a continuous and stable land passage (ca. 2.7 Ma) (Fig. 4). These earliest records of *G. arizonae* extend as far north as 37° N. During the Pleistocene, *Glyptotherium* expanded its longitudinal distribution, until it ranged from 110° W to 80° W (CZAPLEWSKI 2004). Likewise, it dispersed southward into Central America during its cladogenesis, as indicated by records in El Salvador (Irvingtonian?, see CISNEROS 2005) and the late Pleistocene of Honduras and Panamá (WEBB & PERRIGO 1984). In this biogeographic context, the occurrence of *Glyptotherium* cf. *G. cylindricum* in the latest Pleistocene of the northern extreme of South America (Fig. 4) can be interpreted as a new case of re-entrance of a group that emigrated from South America and diversified in North America, as has already been proposed for the pampatheriid Cingulata (SCILLATO-YANÉ et al. 2005). The migratory processes manifested by these Cingulata could be associated with the existence of some kind of low land "corridors" that might have connected the Florida peninsula with Mexico, and/or Central America and the northern extreme of South America (MORGAN & HULBERT 1995; WEBB 2006). These low land "corridors" would have developed during the LGM (Last Glacial Maximum) when the sea level dropped up to 120–140 metres below present sea level (RABASSA et al. 2005). Because the Pliocene vertebrate record of northern South America is so poor, we cannot be sure, if the differentiation of *Glyptotherium* occurred before, with later migration to North America, or vice versa; only new discoveries in northern South America in sediments older, but close to 2.7 Ma, could clarify this situation. In this biogeographic context, CARRANZA-CASTAÑEDA & MILLER (2004) and FLYNN et al. (2005) have reported the presence of the genus *Glyptotherium* in central Mexico, exhumed in sediments dated at approximately 3.9 Ma. Unfortunately, this early Blancan glyptodont material consists primarily of isolated osteoderms (not illustrated), and consequently its generic identification is uncertain to us; it would not be surprising, if this early glyptodontine species record is shown to be related with the new glyptodont we described from the Codore Formation (Pliocene), Falcon State, Venezuela (see CARLINI et al. 2008).

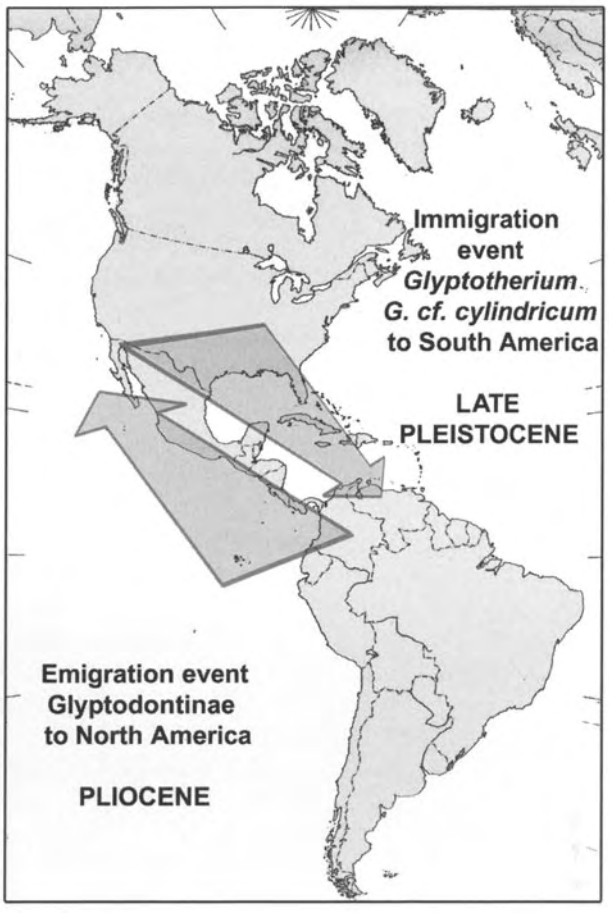

Fig. 4: Main dispersal events of Glyptodontinae between South America and North America: emigration event to North America (Late Pliocene) of a Glyptodontinae species (*Glyptotherium*? sp.) and subsequent differentiation of *Glyptotherium texanum* and immigration event from North America (late Pleistocene) of a *Glyptotherium* species, probably *G.* cf. *cylindricum* and its dispersal to northern South America.

Conclusions

1. The genera *Glyptodon* OWEN, 1839, and *Glyptotherium* OSBORN, 1903, are clearly differentiable taxa. The main distinguishing features are in the

skull-mandible, morphology of the molariforms and osteoderms of the carapace and caudal shield.

2. Biochronologically, the earliest unquestionable records of *Glyptotherium* are about 2.6 Ma old (*G. texanum*), whereas the earliest *Glyptodon* records (*G. munizi*) occur at the early Pleistocene (ca. 1.7 – 0.98 Ma).
3. The presence of *Glyptotherium* cf. *G. cylindricum* in the latest Pleistocene of northernmost South America (Falcón State, Venezuela) suggests a re-entrance of these Glyptodontinae during the late Pleistocene, probably associated with a biogeographical "corridor" that formed during one of the later glacial periods.
4. The assignment of the remains studied to *Glyptotherium* cf. *G. cylindricum* is based primarily on similarities observed in the morphology of the carapace and molariforms, but the relatively poor knowledge of this taxon makes this a tentative assignment. Alternatively, the specimens from Venezuela could correspond to *Glyptotherium floridanum*, a species with an apparently later record (late Rancholabrean), and latitudinal distribution reaching about 33° N.
5. All the records dated in Venezuela are ca. 14 ka, and often associated with some kind of human activity (e.g., TaimaTaima site).

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Additions to the knowledge of *Urumaquia robusta* (Xenarthra, Phyllophaga, Megatheriidae) from the Urumaco Formation (Late Miocene), Estado Falcón, Venezuela

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with 2 figures and 2 tables

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Abstract: We describe new remains of *Urumaquia robusta* CARLINI, BRANDONI & SÁNCHEZ, 2006, which significantly improve the knowledge of the species and allow a more precise discussion about the relationships with the rest of the South American Megatheriinae. The new remains (ulna, phalanx, femora, patella, tibia, astragalus, navicular, metatarsals IV–V) described here suggest close affinities of this taxon with the species of *Pyramiodontherium* and with *Megatheriops rectidens*, based on morphological similarities of the ulna (length, gracility), femur (general morphology, shape of the medial margin), and astragalus (angle between the discoidal and odontoid facets). In fact, the shape of femoral medial margin is a shared derived character among *Urumaquia*, *Pyramiodontherium* and *Megatheriops*. However, and despite the increasing information concerning Tertiary species, their phylogenetic relationships are only partially understood.

Keywords: Megatheriinae • *Urumaquia robusta* • Urumaco Formation • Venezuela • postcranial bones

Kurzfassung: Neue Funde von *Urumaquia robusta* CARLINI, BRANDONI & SÁNCHEZ, 2006 werden vorgestellt, die erheblich zum Verständnis der Art beitragen und eine präzisere Diskussion der Verwandtschaftsverhältnisse zu anderen Vertretern der südamerikanischen Megatheriinae erlauben. Das hierin beschriebene neue Material (Ulna, Phalange, Femura, Patella, Tibia, Astragalus, Navikulare, Metatarsalia IV–V) deutet auf nähere Verwandtschaft zu den Taxa *Pyramiodontherium* und *Megatheriops rectidens* hin. Dies wird unterstützt durch morphologische Ähnlichkeit der Ulna (Länge, Grazilität), des Femurs (generelle Morphologie, Form des medialen Randes) und des Astragalus (Winkel zwischen der Diskoidal- und Odontoidfacette). Tatsächlich handelt es sich bei der Ausprägung des medialen Femurrandes um eine Synapomorphie von *Urumaquia*, *Pyramiodontherium* und *Megatheriops*. Allerdings sind die phylogenetischen Verwandtschaftsverhältnisse, trotz Zunahme von Informationen über tertiäre Taxa, bisher nur teilweise verstanden.

Schlüsselwörter: Megatheriinae • *Urumaquia robusta* • Urumaco Formation • Venezuela • Postcranialelemente

Introduction

For several years, Tertiary xenarthrans from Venezuela were known through a few formally described species, particularly *Urumacotherium garciai* BOCQUENTIN-VILLANUEVA, 1984, from the Urumaco Formation (Late Miocene) (see BOCQUENTIN-VILLANUEVA 1984) and *Asterostemma venezolensis* SIMPSON, 1947, from the Santa Ines Formation (Middle? Miocene) (see SIMPSON 1947). Recent papers mentioned indeterminate Megatherioidea from Middle Miocene sediments of the Castillo Formation (SÁNCHEZ-VILLAGRA et al. 2004) and

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new Mylodontidae from the Urumaco and Codore formations (Late Miocene – Pliocene), Estado Falcón (LINARES 2004). More recently, we reported part of the large diversity of tardigrades we are identifying in three successive Tertiary formations, the Socorro, Urumaco and Codore formations, cropping out in the Estado Falcón, which encompass a temporal lapse from the Middle Miocene to the Pliocene (CARLINI et al. 2005, 2006a, b). Among them, we described the first Megatheriinae from the Tertiary of Venezuela (CARLINI et al. 2006a), represented by two new genera and species from the Late Miocene – Pliocene. For the Urumaco Formation (Late Miocene) we described *Urumaquia robusta* CARLINI, BRANDONI & SÁNCHEZ, 2006, based on few but significant remains (see CARLINI et al. 2006 a) that have been collected in the Urumaco outcrops in the 1970's by a collaborative fieldwork between Venezuelan colleagues and Harvard University (USA).

Brief overviews of the megatheriine remains of the upper Tertiary of South America and their geographic and temporal distribution (CARLINI et al. 2002, 2006a) show that the Tertiary findings were not frequent at low latitudes. More precisely, the new taxa we described in 2006 did not only extend the knowledge of megatheriine diversity in South America, but also led us to speculate about the moment of differentiation of *Megatherium* CUVIER, 1796, and *Eremotherium* SPILLMANN, 1948, both genera with maximum diversity in the Pleistocene. *Urumaquia robusta* is similar in size, and even larger, than the Upper Miocene-Pliocene Argentinean species of the genera *Pyramiodontherium* ROVERETO, 1914, and *Megatheriops* C. AMEGHINO & KRAGLIEVICH, 1921. Some features present in the few materials known so far (location of the navicular facet with respect to the plane of the discoidal facet, and relationship between the ventral portion of the fibular facet and the ectal facet of the astragalus), suggested the possibility that *U. robusta* represents a taxon with an anatomy more derived than that of taxa found in the Middle Miocene of Argentina. The taxa recorded in the Middle Miocene of La Venta, Colombia, most probably were the smallest and most gracile Megatheriinae at the time (see HIRSCHFELD 1985; CARLINI et al. 2006a), being more plesiomorphic than those of Venezuela. Fortunately, in fieldwork carried out during 2005 and 2006, we found more material that can undoubtedly be assigned to *Urumaquia robusta* (that could not be included in the original study). In fact, among the new remains, we found homologous specimens to those of the type specimen (distal tibia and astragalus), which significantly improve the knowledge of the species and allow a discussion of the affinities of the Venezuelan species with the rest of the South American Megatheriinae.

Abbreviations used in the text: AMU-CURS, Colección de Paleontología de Vertebrados de la Alcaldía de Urumaco, Estado Falcón, Venezuela; FMNH, Field Museum of Natural History, Chicago, USA; MACN, Colección de Paleontología de Vertebrados del Museo Argentino de Ciencias Naturales, "Bernardino Rivadavia", Buenos Aires, Argentina; MCN, Museo de Ciencias, Caracas, Venezuela; MLP, Colección de Paleontología de Vertebrados del Museo de Ciencias Naturales de La Plata, La Plata, Argentina; SALMA, South American Land Mammal Age.

Systematic paleontology

Xenarthra COPE, 1889
Phyllophaga OWEN, 1842
Megatherioidea GRAY, 1821
Megatheriidae GRAY, 1821
Megatheriinae GRAY, 1821

Urumaquia robusta CARLINI, BRANDONI & SÁNCHEZ, 2006

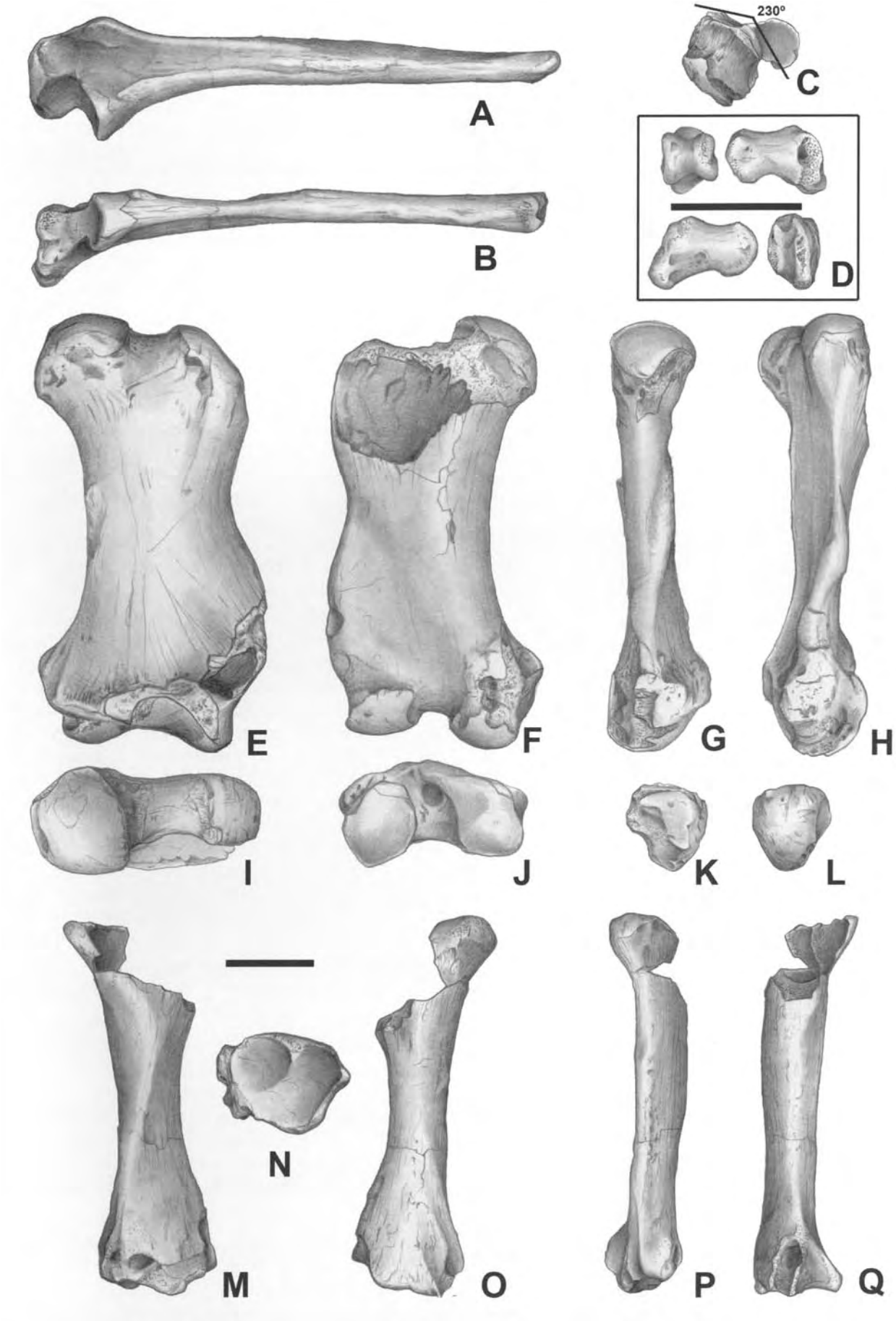
Figs. 1–2

Newly referred material: AMU-CURS 169: right phalanx 1+2 D III (manus), complete left and poorly preserved right femora, right patella, almost complete left tibia, left astragalus, left and right navicular, right metatarsal IV, left metatarsal V; AMU-CURS 176: medial half of the right tibial proximal epiphysis, and complete but crushed right femur; AMU-CURS 179: almost complete left ulna.

Distribution: Urumaco, Estado Falcón, Venezuela; Urumaco Formation, Late Miocene (MINISTERIO DE ENERGÍA Y MINAS 1997; AGUILERA 2004).

Revised diagnosis: A middle- to large-sized Megatheriinae, larger than *Anisodontherium halmyronomum* (CABRERA, 1928), *Megathericulus* AMEGHINO, 1904, *Eomegatherium* KRAGLIEVICH, 1926, *Pliomegatherium* KRAGLIEVICH, 1930, *Promegatherium* AMEGHINO, 1883, and *Eremotherium sefvei* DE IULIIS & SAINT-ANDRÉ, 1997; comparable to *Pyramiodontherium* and some species of *Megatherium* (*M. medinae* PHILLIPPI, 1893; *M. lundi* GERVAIS & AMEGHINO, 1880; *M. tarijense* GERVAIS & AMEGHINO, 1880; and *M. urbinai* PUJOS & SALAS, 2004), smaller than *Megatherium americanum* CUVIER, 1796 and *Megatherium gallardoi* AMEGHINO & KRAGLIEVICH, 1921; *Eremotherium laurillardi* (LUND, 1842) and *Eremotherium eomigrans* DE IULIIS & CARTELLE, 1999. Ulna gracile and slender, much longer than those of other megatheriines (e.g. in *Megatheriops*, *Megatherium* and *Eremotherium*). Femur similar to that of *Pyramiodontherium*, with a slight torsion of the diaphysis of about 22°; the trochanter ma-

Fig. 1. *Urumaquia robusta* (AMU-CURS 179). **A–C**: Left ulna. *Urumaquia robusta* (AMU CURS 169). **D**: Right digit III phalanx 1+2 (manus). **E–J**: Left femur. **K–L**: Right patella. **M–Q**: Left tibia. – **A**, lateral view; **B**, anterior view; **C**, proximal view; **D**, distal, medial, lateral, and proximal views; **E**, anterior view; **F**, posterior view; **G**, medial view; H, lateral view; **I**, proximal view; **J**, distal view; **K**, femoral view; **L**, anterior view; **M**, anterior view; **N**, distal view; **O**, posterior view; **P**, medial view; **Q**, lateral view. – Scale bar = 100 mm.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jor proportionally less developed than in *Pyramiodontherium*, and with the medial margin of the diaphysis concave. Tibia distally very thick, and with shallow grooves for the foot extensor tendons (shallower than in *Megatherium* and *Eremotherium*). The angle between the odontoid and discoid facets in the astragalus is approximately 100° (90° in *Pyramiodontherium bergi* and *P. scillatoyanei*, between 100° and 120° in *Megatherium* and *Eremotherium laurillardi*). The astragalar depression is deep and conical with a very sharp apex. Nearly one half of the navicular facet is dorsal with respect to the plane of the discoid facet, whereas in *Pyramiodontherium* spp., *E. laurillardi* and *Megatherium urbinai*, only one third is dorsal to this plane. Humerus with a prominent deltopectoral crest, as in *Megathericulus*, *Pyramiodontherium* and *Megatheriops*, (virtually absent in *Megatherium* and *Eremotherium*). Metatarsal III with two subcircular areas forming the ectocuneiform facet. Distal surface to digit III slightly convex dorsoventrally, entirely articular and inclined along a dorsolateral to ventromedial axis.

Description

Ulna: The ulna (AMU-CURS 179) (600 mm lenght) is very gracile and proportionally much longer than those of any other megatheriine (e.g. in *Megatheriops*, *Megatherium* and *Eremotherium*); it is straight, thinning toward the distal end and thickening proximally (being always gracile) toward a massive but short olecranon process (Figs. 1A–C). Unlike most megatheriines, and similar to FMNH P14511, the distal epiphysis is not widened, whereas the diaphysis continues narrowing up to the distal end. As in other megatheriines, it has a proximal facet for the humerus divided into two areas (one for the condyle and another for the trochlea), that form an angle of about 230°, and another proximal facet for the radius.

Digit III P 1+2 (manus): Digit III is the strongest anterior clawed digit in Megatheriinae. It is composed of a single proximal bone (fused phalanxes 1+2?, as has been proposed for the other megatheriines) (Fig. 1D), and a strong ungual phalanx that is claw-shaped. The proximal surface of the phalanx 1+2 seems to be more elongate than in other megatheriines (e.g., *Megatherium*), and bears a wide facet for metacarpal III. This facet is canal-shaped and elongated along the dorsolateral-ventromedial axis. A small, transverse, non-articular distinct ridge-like bone subdivides it into two areas, the upper one is concave and oval in section (in *Megatherium* and *Eremotherium* the ridge-like non articular bone is more developed). The distal surface bears an asymmetric trochlea and an incomplete vertical non-articular bony area between the semicircular condyles. The phalanx is slightly oriented medially and, consequently, the ungual phalanx is deviated ventromedially.

Femur: The femur of *Urumaquia robusta* (AMU-CURS 169) is morphologically similar to that of the species of *Pyramiodontherium* (Figs. 1E-J). Its total length is 500 mm and the minimum transverse diameter at the middle of the diaphysis is 155 mm (see Tab. 1); it is transversally expanded both in the proximal and distal portions. The torsion of the diaphysis is clearly less (approx. 22°) than in the other species of Megatheriinae (e.g. *Megatherium americanum*, *Pyramiodontherium bergi*) (Figs. 1G–H). In *P. bergi* this torsion is approximately 40° between the proximal and distal epiphysial axes; in *M. americanum* it varies between 31° and 57°; in *Eremotherium laurillardi* between 10° and 41° (DE IULIIS 1996; DE IULIIS et al. 2004). The articular surface of the femoral head is clearly defined proximally by a distinctive neck, as in *P. scillatoyanei* (MLP 68-III-14-1), and not as in *P. brevirostrum* (MLP 31-XI-12-25). The trochanter major is proportionally less developed than those of the *Pyramiodontherium* spp., where it is more outward extended. As in the species of *Pyramiodontherium*, *Megatherium americanum* and *M. sundti* PHILIPPI, 1893 (DE IULIIS 2006: fig. 2C), the medial margin of the diaphysis is concave in *Urumaquia robusta* (Figs. 1E–F), whereas in *Eremotherium laurillardi*, *Eremotherium sefvei* (DE IULIIS & SAINT ANDRÉ 1997: figs. 4 and 5, respectively), *Eremotherium eomigrans* (DE IULIIS & CARTELLE 1999: fig. 5a), and *Megatherium medinae* (CASAMIQUELA & SEPÚLVEDA 1974: fig. 6) both the lateral and medial margins are subparallel. In *Urumaquia robusta*, and as in most megatheriines, the patellar facet is separated from the internal condyle and continuous with the external condyle, forming a single articular surface (Figs. 1E, J), whereas in *Megathericulus patagonicus* AMEGHINO, 1904 (MLP 92-XI-15-2), and *Megathericulus primaevus* CABRERA, 1939 (MLP 39-VI-24-1), it is connected with both condyles. In *U. robusta* the patellar facet is more developed than in *Pyramiodontherium bergi*, and contrary to *Megatherium americanum*, it is widely continuous with the lateral condyle. However, the limits of the patellar facet are indicated by a slight difference in the level with the end of the condylar area (Fig. 1J). The ectepicondyle is massive, although not as much as in *Pyramiodontherium brevirostrum*.

Patella: Associated with the remains AMU-CURS 169 there is an almost complete right patella, which has the medial third of the articular surface partially eroded (Figs. 1K–L). It is subtriangular, with the apex toward the tibia and a wide proximal base. The external surface is rugose, and the femoral facet is almost flat and asymmetrical, displaced laterally. It is similar to that of some specimens of *E. laurillardi*, although there seems to be a large variability in shape and size in the patellae of the latter species.

Tibia: Two remains of tibiae of two different specimens are known besides the type specimen (MCN 91-72v); one (AMU-CURS 169) is almost complete, but lacks the external portion of the proximal epiphysis (Figs. 1M–Q), the other one is represented only by the

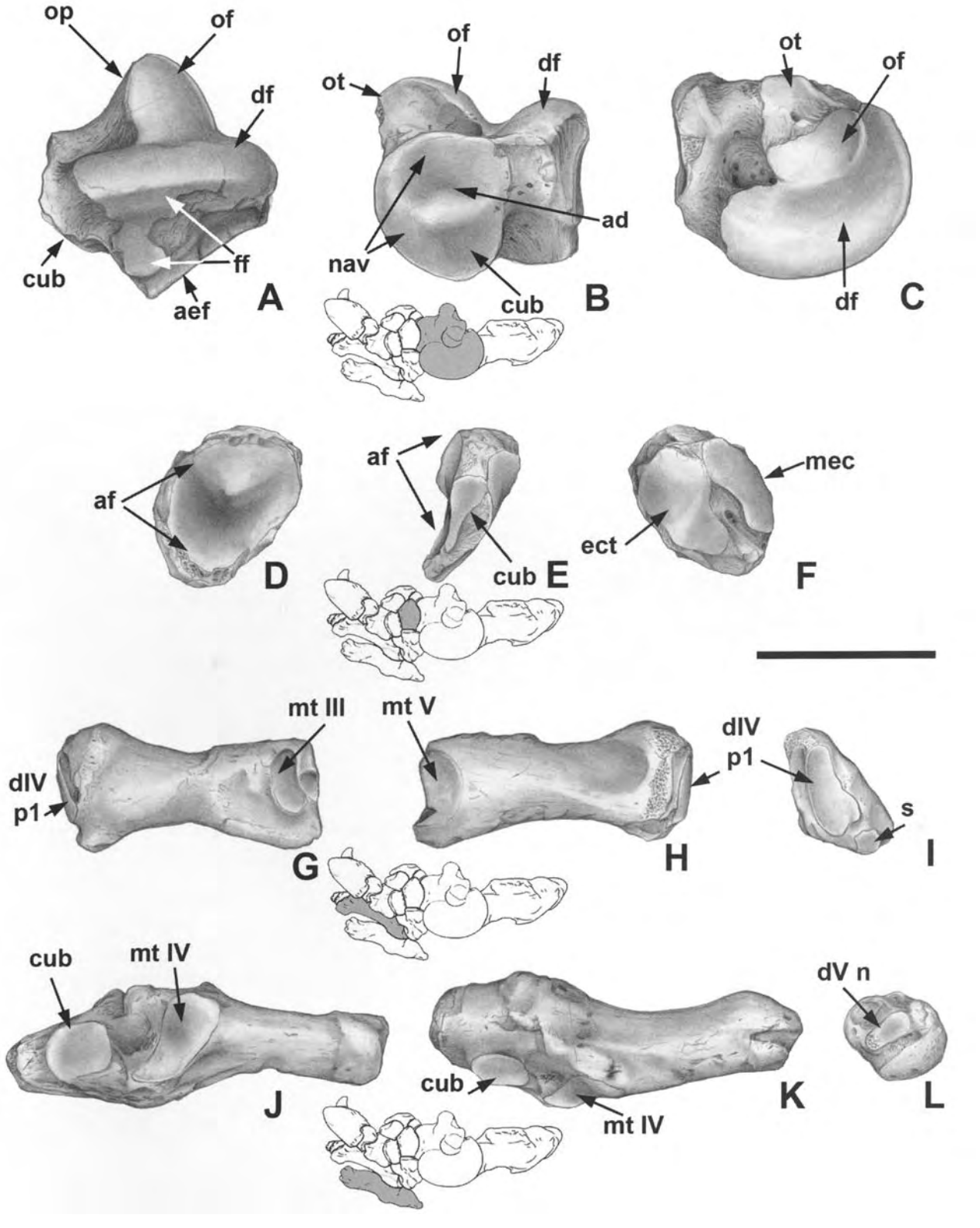

Fig. 2. *Urumaquia robusta* (AMU-CURS 169). **A–C**: Left astragalus. **D–F**: Right navicular. **G–I**: Right metatarsal IV. **J–L**: Left metatarsal V. – **A**, dorsolateral view; **B**, anterior view; **C,** dorsomedial view; **D**, proximal view; **E**, lateral view; **F**, distal view; **G**, medial view; **H**, lateral view; **I**, distal view; **J**, medial view; **K**, dorsal view; **L**, distal view. – Abbreviations: **ad**, astragalar depresion; **aef**, astragalar ectal facet; **af**, astragalar facet; **cub**: cuboid facet; **df**: discoid facet; **dIV p1**, digit IV phalanx 1; **dV n**, digit V, nodular facet; **ect**, ectocuneiform facet; **ff**: fibular facet; **mec**, meso-entocuneiform complex facet; **mt III**, metatarsal III facet; **mt IV**, metatarsal IV facet; **mt V**, metatarsal V facet; **nav**: navicular facet; **of**: odontoid facet; **op**: odontoid process; **ot**: odontoid tuberosity; **s**, sesamoid facet. – Scale bar = 100 mm.

Tab. 1. Femur measurements in mm. * from DE IULIIS (1996).

Taxon	Specimen	Length (L)	Proximal width	Distal width	Diaphysis medial width
Pyramiodontherium scillatoyanei	MLP 68-III-14-1	473	263	257	155
Pyramiodontherium bergi	MLP 2-66	515	305	280	190
Pyramiodontherium brevirostrum	MLP 31-XI-12-25	580	300	285	180
Pyramiodontherium sp.	MLP 31-XI-12-26	482	230	245	166
Pyramiodontherium sp.	MACN Pv-2817	597	360	350	210
Megatherium	Sta. Rosa (Tastil)	565	310	320	250
Megatherium lundi	(Museo de Salto)	570	325	310	200
Megatherium lundi	MLP 2-30	575	299	312	211
Megatherium lundi	MLP 2-31	605	328	344	220
Megatherium tarijense *	FMNH P 14216	528	273	266	200
Megatherium americanum *	MLP 2-207	735	431	403	260
Megatherium americanum *	MLP 2-29	759	459	473	311
Megatherium americanum *	MLP sala9	712	392	409	270
Megatherium americanum *	MLP 44-XII-28-1	660	390	390	285
Megatherium americanum	CC 1008	620	350	330	220
Urumaquia robusta	AMU-CURS 169	500	230	250	160
Urumaquia robusta	AMU-CURS 176	475	225	248	140

partial proximal portion (AMU-CURS 176). The tibia of *Urumaquia robusta* is long, as in other Tertiary megatheriines, with a minimum total length of 440 mm and a minimum transverse width of the diaphysis of 65 mm (AMU-CURS 169); the relationship tibia length/femur length is similar to that of *P. brevirostrum*, and lower than in *P. bergi* and *P. scillatoyanei* (see Tab. 2). The proximal articular surface has a markedly concave internal condylar facet, which is oval in shape; the longitudinal axis is oblique, forming an angle of approximately 45° with the transverse axis. The cnemial crest of *U. robusta* (Fig. 1M) is not as marked as in *P. bergi*, but the middle section of the diaphysis is subtriangular as in this latter species; in contrast, the tibia is oval in section in several specimens of *Megatherium americanum* and *Pyramiodontherium scillatoyanei* (MLP 68-III-14-1). As in the type specimen, the distal epiphysis is thick, without the strong differences in diameter between the epiphysis and the distal diaphysis observed in most other megatheriines. The two shallow tendinous grooves for the digital flexors, limited by three crests, are well distinguishable (Figs. 1O–P). The astragalar facet of the tibia (Fig. 1N) has a wide facet for the odontoid process, as in *P. brevirostrum* (MLP 31-XI-12-25) and *P. scillatoyanei* (MLP 68-III-14-1) (similar to most Quaternary taxa), and is relatively wider than that of *P. bergi* (MLP 2-66). The discoid facet is similar in development to species of *Pyramiodontherium*. The angle between both facets is approximately 106°, while it is 135° in *Megathericulus patagonicus* (MLP 91-IX-7-18, MLP 92-XI-15-2), 114° in *P. brevirostrum* and 87° in *P. bergi*.

Astragalus: The astragalus has the typical shape for Megatheriinae (see BRANDONI et al. 2004). It is massive, with a well-developed central odontoid process in dorsomedial view (Figs. 2A–C) and a navicular facet in anterior view (Fig. 2B). As in other megatheriines, the fibular facet is divided into two main areas (Fig. 2A), an anteroposteriorly elongated dorsal portion (that joins the discoid facet dorsally) and a ventral facet with a rounded surface slightly extended ventrally. A similar general shape can be observed in *Pyramiodontherium bergi* (MLP 2-66) and in *P. scillatoyanei* (MLP 68-III-14-1), but in *P. scillatoyanei*, and also in *Eomegatherium nanum* (BURMEISTER 1891) (MACN Pv-4992), the ventral portion of the fibular facet is rather circular and more oval, with the long axis perpendicular to the discoid facet with a reduced dorsal portion (see BRANDONI et al. 2004). In the oldest well-known Megatheriinae, *Megathericulus patagonicus*, the ventral part of the fibular facet reaches the ectal facet.

In *Urumaquia robusta* (AMU-CURS 169) the complete odontoid process with the odontoid facet is

Tab. 2. Tibia measurements in mm. * from DE IULIIS (1996).

Taxon	Specimen	Length (L)	Proximal width	Distal width	Diaphysis medial width	Tibia L / Femur L
Megathericulus patagonicus	MLP 91-IX-7-18	270	120 aprox	150	55	
Pyramiodontherium bergi	MLP 2-66 L	514	230	222	87	0.99
Pyramiodontherium bergi	MLP 2-66 R		220	210	90	
Pyramiodontherium brevirostrum	MLP 31-XI-25	500	210	170		0.86
Pyramiodontherium scillatoyanei	MLP 68-III-14-1	472	215	205	81	0.99
Pyramiodontherium	MLP 31-XI-12-26 L	425	195	150		0.88
Pyramiodontherium	MLP 31-XI-12-26 R	435	180	160		
Megatherium lundi	MLP 2-30	446	246	222	81	0.77
Megatherium lundi	MLP 2-31	445	235	245	97	0.73
Megatherium lundi	(Museo de Salto)	450	245	235	89	0.79
Megatherium	Sta Rosa (Tastil)	510	265	247	97	0.9
Megatherium americanum *	MLP 2-207	560	360		115	0.76
Megatherium americanum *	MLP 2-29	620	355	305	141	0.81
Megatherium americanum *	MLP 2-79	539	342		123	
Megatherium americanum *	MLP sala9	568	330	290	100	0.79
Megatherium americanum *	MLP 44-XII-28-1	550	302	290	120	0.83
Megatherium americanum *	MACN Pv-10147	475	275		112	
Megatherium tarijense *	FMNH P 14216	408	214	202	85	0.77
Urumaquia robusta	MCN 91-72v (type)			167		
Urumaquia robusta	AMU-CURS 169	440		130	69	0.88

preserved. The angle between the odontoid and discoid facets is approximately 100° (Fig. 2B), as in the type specimen. The facet for the navicular, on the anteriormost part of the astragalus, has its major axis oriented dorsolaterally to ventromedially. The concave dorsolateral portion of the navicular facet, termed the astragalar depression (see Fig. 2B), is more circular in section than that of *P. bergi* (see BRANDONI et al. 2004). The astragalar depression is deep as in *P. bergi*, *P. scillatoyanei*, and *Eomegatherium nanum*, but conical with a very sharp, pointed apex. In *U. robusta* about one-half of the navicular facet is positioned dorsally with respect to the plane of the discoid facet, similar to *Megathericulus patagonicus*. In *Pyramiodontherium* spp., *Eremotherium laurillardi*, and *Megatherium urbinai*, only one-third is dorsally located. In contrast, in *M. americanum* the top of the dorsomedial part of the navicular facet is at the same level with the discoid facet plane. There are two facets for articulation with the calcaneum, the reduced sustentacular facet and the large and concave ectal facet, separated by a deep and wide nonarticular bony canal, the sulcus tali.

Navicular: The navicular (Figs. 2D–F) is oval to subrectangular in shape (distal view) and antero-posteriorly compressed, with the main axis oriented dorsolaterally to ventromedially (DE IULIIS 1996; BRANDONI et al. 2004). The astragalar facet (Fig. 2D) is located on the proximal surface, and can be differentiated into dorsolateral and ventromedial halves. The dorsolateral half is more or less subcircular in the outer section, but is eccentrically conic resulting in a subtriangular shape; instead in *P. bergi* and *M. americanum* it is subcircular and forms a prominent condylar projection that fits into the circular depression of the astragalus. This projection is well developed, but not as in *M. americanum*. The ventromedial half is semilunar, concave along its main axes and articulates with the condylar portion of the astragalus. As in *P. bergi* and *M. americanum*, both halves are similar in size; in *M. altiplanicum* from the Pliocene of Bolivia, the medial part of the facet is larger than the lateral part (SAINT-ANDRÉ & DE IULIIS 2001).

A cuboid facet lies on the ventrolateral portion of the navicular (Fig. 2E). It is elongate along the dorsolateral-ventromedial axis. In *Urumaquia robusta* and *Megatherium americanum* the cuboid facet is located in

a single plane. In *P. bergi*, this facet has two different portions, one dorsolateral and another ventral (see BRANDONI et al. 2004).

On the distal surface, the navicular is convex along its main axes (Fig. 2E). As in *M. americanum*, there are two articular facets (Fig. 2F), ventrally the ectocuneiform facet and dorsomedially the meso-entocuneiforms facet; in *P. bergi* there are instead three, because the ventral facet is divided in two (see BRANDONI et al. 2004).

Metatarsal IV: Metatarsal IV (Figs. 2G–I) is long and not as compressed as metatarsal III (see CARLINI et al. 2006a). The diaphysis is laterally oriented triangular in section, whereas in *M. americanum* the section is subtriangular to oval. Proximally, two articular facets are preserved, an anteromedial facet for Mt III (Fig. 2G) and a lateral facet for Mt V (Fig. 2H), The facet for the cuboid is not preserved, because the bone is broken. The facet for Mt III is oval, dorsoventrally extended, and slightly concave in both directions. The facet for Mt V is located on the external side of the proximal epiphysis. This facet is subcircular and flat. The distal epiphysis is triangular, with a laterodorsal apex and a tripod-like base (Fig. 2I). The facet for the proximal phalanx of digit IV is crested, as that for metatarsal III, but less acute in section, and narrowing ventrally. Ventromedially there is a small and convex subcircular facet for a sesamoid.

Metatarsal V: Metatarsal V (Figs. 2J–L) is slightly longer than metatarsal IV, but depressed dorsoplantarly, with the lateral margin expanded and dorsoventrally compressed (especially the proximal two-thirds). The distal portion is almost isodiametric. The medial side has two continuous articular facets that are inclined dorsomedially. The anteriormost facet for Mt IV is subtriangular, with a ventroposterior apex, relatively flat, and not continuous posteriorly with the cuboid facet (Figs. J–K). The cuboid facet is slightly concave and squared. The posterior end of metatarsal V is not prominent and point-shaped, as in *P. bergi*. The distal surface (Fig. 2L) has a very small oval and convex, elongated facet along the dorsolateral-ventromedial axis for a nodular vestigial phalanx, the latter smaller than that of *P. bergi*.

Discussion

The most ancient records of the subfamily Megatheriinae are as old as the Middle Miocene of Patagonia (Argentina), and include the genera of the "Friasian" lapse (sensu lato), represented in South America by three successive faunas, the Colloncuran, Laventan and Mayoan faunas. HIRSCHFELD (1985) reported megatheriine remains from the Laventan SALMA of Colombia. Hence, for the Miocene, the fossil record suggests that the Megatheriinae were distributed at least in north-western South America and western Patagonia. The megatheriines of La Venta (Colombia) have not been fully studied yet; however, in view of the few published data, there are two taxa related to *Megathericulus* (cf. *M. patagonicus*) and *Eomegatherium* (cf. *Eo. andinum* KRAGLIEVICH, 1930, *Eo. cabrerai*), both also recorded in the Mayoan of Patagonia (KRAGLIEVICH 1930; SCILLATO-YANÉ et al. 1993; BRANDONI & CARLINI 2004). Thus, Megatheriinae were probably distributed homogeneously along the west of the continent (CARLINI et al. 2006a) in the Middle Miocene in South America, although a wider distribution encompassing the whole of South America cannot be discarded. Concerning the geographic relationship between Patagonia and La Venta, CANDELA & MORRONE (2003: 373) stated: "Más allá de estas incertidumbres, las similitudes faunísticas entre La Venta y las mencionadas faunas fósiles de Argentina, expresadas aquí en el trazo I, indican que ellas serían las descendientes de una biota ancestral ampliamente distribuida en el pasado" ("These uncertainties aside, the faunistic similarities between La Venta and the faunas from Argentina mentioned above, expressed here in the 'trazo 1', indicate that they would be descendants from an ancestral biota of wide distribution in the past"). In this sense, most Tertiary Megatheriinae are distributed along the "trazo generalizado I" of CANDELA & MORRONE (2003: fig. 7).

The information about the Megatheriinae recorded in northern South America is very scarce. Recently, CARLINI et al. (2006a) described two new Megatheriinae from the Late Miocene-Pliocene of Venezuela. The new remains of *Urumaquia robusta* here described suggest closer affinities of this taxon with the species of *Pyramiodontherium* and *Megatheriops rectidens* (ROVERETO 1914), based on morphological similarities of the ulna (length, gracility), femur (general morphology, shape of the medial margin), and astragalus (angle between the discoidal and odontoid facets). In fact, the shape of femoral medial margin is a shared derived character among *Urumaquia*, *Pyramiodontherium* and *Megatheriops*. However, and despite the increasing information concerning Tertiary species, the phylogenetic relationships among them are only partially understood (BRANDONI 2006; PUJOS 2006), mainly because of the absence of enough data for the analysis (BRANDONI 2006).

Hence, it is very likely that the history of Megatheriinae in northern South America began with some taxon closely related to the primitive Patagonian megatheriines (*Megathericulus*, *Eomegatherium*), which then further diverged into a group (*Urumaquia*) related to the clade *Pyramiodontherium-Megatheriops* (see BRANDONI 2006; PUJOS 2006), and finally gave rise to the phyletic series proposed by CARLINI et al. (2006a) (i.e. *Proeremotherium-Eremotherium*). These authors considered *Proeremotherium eljebe* CARLINI, BRANDONI & SÁNCHEZ, 2006, as the taxon basal to *Eremotherium*, the latter representing the mainly Pleistocene megatheriine widely distributed in southern North America, Central

America, and lowlands of northern and eastern South America. It might be possible that, as in Glyptodontinae (see CARLINI et al. this volume), Megatheriinae (*Proeremotherium* sp.?) migrated to North America after the Panama isthmus was definitively established in the Late Pliocene (ca. 2.7 Ma, see WOODBURNE et al. 2006), gave rise to *Eremotherium* there, and then this last genus re-entered South America some time during the Pleistocene. If so, this is another case of xenarthran cladogenetic processes in North America after the Late Pliocene, that led to taxa that re-entered South America, as in the Pampatheridae (*Holmesina* SIMPSON, 1930; see SCILLATO-YANÉ et al. 2005) and Glyptodontinae (*Glyptotherium* OSBORN, 1903; see CARLINI et al. 2008).

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Future perspectives

It has been stated that intertropical South America has behaved as a reservoir for taxa that had already became extinct in southern South America (Goin and Candela, 2004; Hadler et al., 2008). The xenarthran assemblages from the Neogene of Venezuela reported in this thesis provide new cases of this phenomenon. This constitutes then another example of the tropics as 'cradle and museums' of biodiversity (Jablonski et al. 2006). In sum, the research presented in this thesis is an example of the great unknown taxonomic and morphological richness that the exploration of vertebrates in the northern Neotropics can reveal.

Cenozoic fossil land mammals have an excellent record in the austral part of the South American Continent (Pascual et al., 1996; Ortiz Jaureguízar and Cladera, 2006). It was upon this record that South American biochronology and the concept of South American Land mammal Ages was based. However, it is evident that the biochronology and main mammal evolutionary steps so far proposed are not necessarily valid for the entire continent (Pascual et al., 1996; Ortiz Jaureguízar and Cladera, 2006), at least as they have been traditionally interpreted. What the growing palaeontological record of the northern Neotropics will mean for biostratigraphic practice in South America remains to be seen. Clearly the 'Land mammal ages' are useful categorisations for comparisons and discoveries of differences and incongruencies in the record, but much less useful as biochronological reference in continent-wide research.

The most fundamental way in which further hypotheses on mammalian evolution can be tested, such as the origin of the Greater Antilles fauna, is through new discoveries resulting from new fieldwork efforts in key locations, and in this regard Venezuela offers many potential sites (Sánchez-Villagra et al. 2010). Another area is of course the revision of known faunas, including studies of anatomy and phylogeny of critical groups. The use of non-invasive imaging

techniques is having a major impact on current palaeontological research (Zollikofer and Ponce de León 2005), and this is also affecting research on xenarthran evolution. We are currently using computer tomography imaging to study Venezuelan fossil glyptodonts and discovering a whole new set of anatomical features very useful to address palaeobiological questions. For example, the complex anatomy of turbinal bones of the ethmoidal region offers insights into thermoregulatory and olfactory adaptations, and visualising this region becomes feasible only with non-invasive imaging.

Another area of large potential of productive investigations on xenarthran evolution is developmental evolution. For example, studies of the vertebral column are of particular interest (Galliari et al. 2010), as xenarthrans show a high degree of polymorphism in this area and seem to have overcome some of the developmental constraints that affect vertebral evolution across Mammalia. Müller et al. (2010) recently showed how fossils can very much contribute to this kind of study due to the correlation between vertebral numbers and identity with somitogenesis and homeotic gene expression.

The Quaternary ground sloth *Megatherium americanum* Cuvier, 1796 was the first fossil mammal to be described from South America (Hoffstetter 1982). Since then, much has been discovered in the southern extremes of the continent, studies which have been mostly taxonomic in scope. With the advent of new imaging techniques, analytical methods to study phylogeny and palaeobiology, and with new discoveries from lower latitudes, a small revolution in our knowledge of fossil xenarthran mammals and other extinct fossil groups from South America is likely to occur.

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Appendix

Book chapter *in press* in *Urumaco and Venezuelan Palaeontology – The fossil record of the Northern Neotropics,* Indiana University Press (Sánchez-Villagra MR, Aguilera O, Carlini AA, eds)

The fossil vertebrate record of Venezuela of the last 65 million years.

Article *published* in *Acta Zoologica* (Krmpotic et al. 2009, Vol. 90/4, pp. 339-351)

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Galliari FC, Carlini AC, Sánchez-Villagra MR. 2010. Evolution of the axial skeleton in armadillos (Mammalia, Dasypodidae)

THE FOSSIL VERTEBRATE RECORD OF VENEZUELA OF THE LAST 65 MILLION YEARS

3

Marcelo R. Sánchez-Villagra, Orangel A. Aguilera,
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In his 1940 "Review of the mammal-bearing Tertiary of South America," G. G. Simpson summarized the scanty record of Venezuela (703–704): "Few as discoveries are, they are important because they show unquestionable affinities with fossil mammals of Argentina and none with those of North America. In view of the fact that no South American mammals had reached North America in the Miocene or earliest Pliocene, even this small budget of evidence is enough to prove that South America was then a unified continent with its northern and southern parts united by land and that the northern part, as well as the southern, was then separated from North America by a marine barrier." What little was known about northern neotropical vertebrate paleontology in 1940 was already important in addressing some large issues about biogeography and the past history of the American continent. Vertebrate paleontology in Venezuela is still in a descriptive phase, but the number of discoveries has increased exponentially in the last few years, and contributions in this volume exemplify how some of them are being used to address fundamental issues about evolution in the tropics and major events in vertebrate evolution, such as the Great American Biotic Interchange in both terrestrial and marine habitats.

Here we present a chronological review of Venezuelan formations and sites with reported fossil vertebrates. Many of the sites and their fossils are also discussed specifically in different chapters of this book.

Paleogene vertebrates from Venezuela are almost unknown. Several aspects on paleoenvironments and palynology of the Paleocene and Eocene of Venezuela were discussed by Rull (2000). There are several Neogene fossil sites, but most are poorly known localities with only one or a few taxa or remains reported. By far the most important section with vertebrates in the Cenozoic of Venezuela is that of the Urumaco sequence, the geology of which is treated in a separate chapter (Quiroz and Jaramillo this volume). Most vertebrate faunas from the Neogene show very low diversity, with the sole exception of the Urumaco sequence and the Cerro La Cruz site. Faunas with vertebrates are found in the Guárico sub-basin, Barinas basin, and Falcón basin. Pleistocene and Holocene deposits are becoming better known, and as discussed below the recently

discovered tar pits in Zulia state and the archeological sites in Falcón state are the most significant sites.

Many of the fossils mentioned below are in collections in Europe and the USA. In Venezuela, vertebrate fossils are reposited principally in the following institutions: Collection of Vertebrate Paleontology of the Alcaldía del Urumaco, Estado Falcón (AMU-CURS); Centro de Historia de la Ciudad de Trujillo, Colección de Geología y Paleontología (CH-V); Centro de Investigaciones Antropológicas, Arqueológicas, y Paleontológicas, Coro (CIAAP); Museo de Biología de la Universidad del Zulia, Paleontología (MBLUZ-P); Museo de Ciencias Naturales de Caracas (MCNC); Universidad Nacional Experimental Francisco de Miranda, Coro (UNEFM); Universidad Nacional Experimental Francisco de Miranda, Coro / Centro de Investigaciones Antropológicas, Arqueológicas y Paleontológicas, Coro (UNEFM-CIAAP); Universidad Simón Bolívar, Laboratorio de Paleobiología (USB-PB).

Sedimentary Basins of Venezuela

The sedimentary basins of Venezuela (fig. 3.1) contain large volumes of oil, and this has led to long-standing great interest in the Venezuelan geology (Tankard, Suárez, and Welsink 1995). In northern Venezuela, uplift events range in time from the latest Eocene through the present, producing sediments that were arranged in molasse cycles (Macsotay et al. 1995).

From west to east, orogenic phases produced the Mérida Andes, Coastal Range ("Caribbean Mountains"), Eastern Interior, Araya-Paria, and Northern and Central Ranges of Trinidad. The molasse cycles attained several kilometers' thickness of sediments, many of which contain fossil vertebrates. Of particular interest is the Falcón basin, one of the major sedimentary regions in the Cenozoic of Venezuela (fig. 3.1).

Several formations in this basin are rich in fossil vertebrates. Recognizing these formations is sometimes a nomenclatural issue, although the geology of the region is well mapped. Approximately 40% of the formation names used by Liddle (1946) for Venezuela in the classic work *The Geology of Venezuela and Trinidad* are no longer in use. The "Léxico Estratigráfico de Venezuela" (Ministerio de Energía y Minas 1997) has a list of synonymies for each valid formation. Identification of formations has been and continues to be a matter of controversy among stratigraphers in Venezuela—the discrepancies reflect very much different philosophies on what a formation is, in addition to nomenclatural issues, which in many cases have also played a role. Geologists with a European background have tended to see formations as chronostratigraphic units, whereas those with an American background see them as lithostratigraphic units.

Castillo Formation—Late Oligocene and Early Miocene of the Falcón Basin

Sánchez-Villagra et al. (2000) first reported a new fossil fauna and flora from Lara state, and contributions in Sánchez-Villagra et al. (2001) and Sánchez-Villagra and Clack (2004) described several aspects of this fauna in detail. These fossils are from the Castillo Formation, which was named

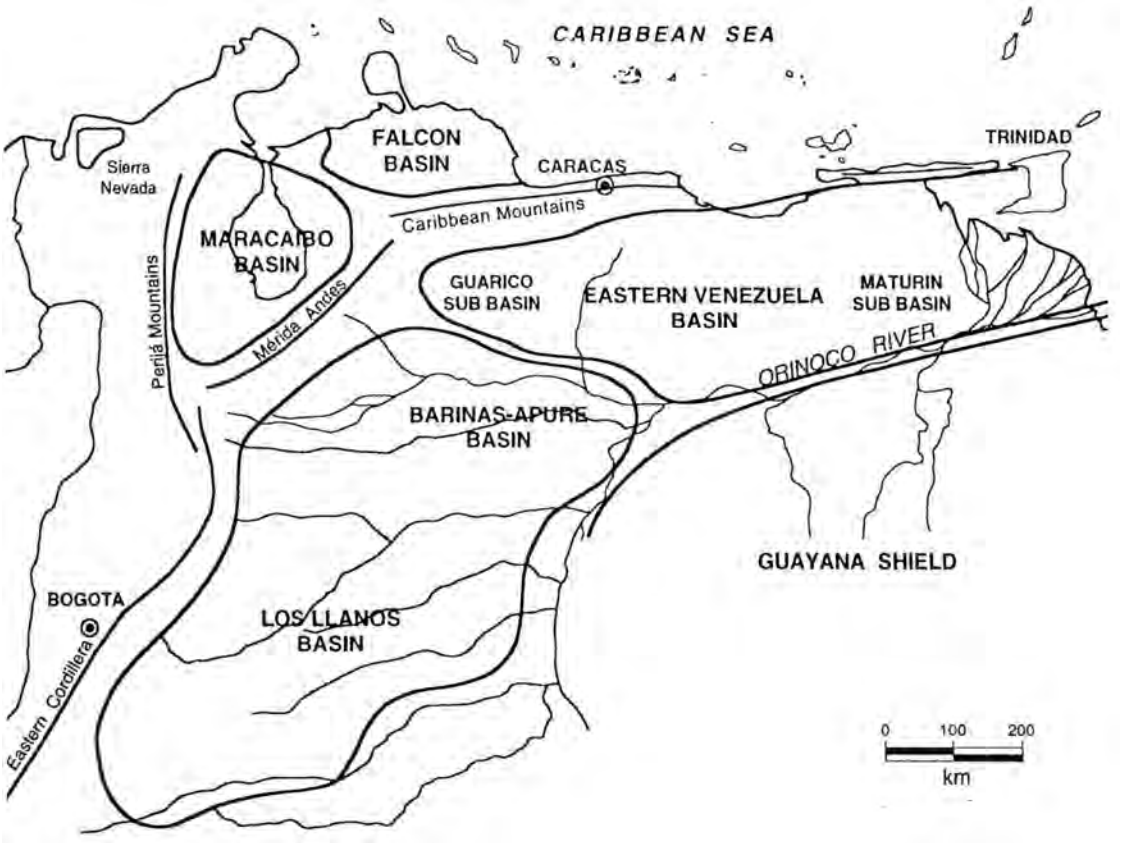


Fig. 3.1. The Cenozoic sedimentary basins of Venezuela and eastern Colombia. *Modified from Díaz de Gamero (1996).*

by Wheeler (1960, 1963) after the Cerro Castillo, about 27 km south of Dabajuro, Distrito Buchivacoa, Estado Falcón. The formation is exposed in a semicircular area along the western edge of the Falcón basin and disappears toward the center of the basin. According to Wheeler (1960), based on study of foraminifera and macroinvertebrates, the fauna of the type locality of the Castillo Formation indicates a Late Oligocene age; sections south of this locality also include younger rocks, extending to the Early Miocene. Cati et al. (1968) considered the entire Castillo Formation to be of Early Miocene age.

There are extensive exposures of the Castillo Formation in Lara and Falcón states, but most of the vertebrate discoveries from this formation have been made in a relatively small area, the Cerro La Cruz locality (Sánchez-Villagra et al. 2004). The latter consists of more than 100 m of section exposed in an area of about 2 km2, located on the southern flank of the Serranía La Baragua, in the northwestern area of Lara state, approximately 4 km northwest from Caserío La Mesa. It can be reached by the road between La Mesa and San Jacinto. Coordinates for the site are latitude 10° 22' N, longitude 70° 03' W. The Cerro La Cruz section consists of ca. 87 m of clayey marls interbedded with numerous thin (<1m thick) hardground units. The strata are underlain and overlain by sandstones, and the upper 15 m are gypsiferous. The strata are steeply dipping, and more than 100 m of section are exposed in an area of about 1 km^2. A

stratigraphic section of the locality was illustrated by Sánchez-Villagra et al. (2001).

Both Wheeler (1960) and Cati et al. (1968) suggested an Early Miocene age for the exposures of the Castillo Formation at Cerro La Cruz, an estimate consistent with vertebrate and invertebrate remains reported by Sánchez-Villagra et al. (2000, 2001, 2004). In the vicinity of the fossil locality, the Castillo Formation lies unconformably over Eocene rocks of the Misoa Formation (Wheeler 1960, 1963; Patterson 1977; Stephan 1977). However, the contact of the Castillo Formation with the overlying or underlying formations cannot be seen at Cerro La Cruz. About 500 m northward from Cerro La Cruz, the underlying Eocene Misoa Formation is exposed, consisting of mostly gray shales with some marine fossils.

A complete faunal list of vertebrates thus far reported for the Cerro La Cruz and Siquisique localities is presented in table 3.1. The Cerro La Cruz locality preserves a fauna from a shallow marine environment at what is today an arid inland region in the Falcón Basin. It formerly lay north of the fork of land that divided this area from the Orinoco Seaway (cf. Iturralde-Vinent and MacPhee 1999: figs. 7, 8). Currently northwestern Lara state is arid, and its drainage basins are small, with rivers of low, intermittent discharge.

Different aspects of the Cerro La Cruz fauna provide clues for a paleoenvironmental reconstruction. The molluscan fauna indicates a calm-water environment with fine-grained sediment; many recent species in the same genera are confined to shallow tropical water of normal salinity. The cosmopolitan crab genus *Portunus* embraces numerous recent species of actively swimming crabs that are typically found in shallow-water habitats, often on sandy or coralline substrates (Rathbun 1920). If the ecological preferences of the shark taxa have not changed since the Late Oligocene, they suggest that the Cerro La Cruz environment of deposition was a tropical shallow sea. The ecology of the pelomedusoides from Cerro La Cruz (*Bairdemys*) is not well known, but Winkler and Sánchez-Villagra (2006) reported marine habits for species of this genus from the Late Miocene Urumaco Formation based on the discovery of a nesting site. In conclusion, all faunal elements either suggest or are consistent with a coastal marine environment of deposition. All marine fishes reported from Cerro La Cruz (Sánchez-Villagra et al. 2000; Aguilera and Lundberg this volume) prefer warm and shallow water environments. The occurrence of a sirenian and a crocodile (Brochu and Rincón 2004) suggests a warm climate, as is expected for a locality at this latitude.

Reconstructions of the changing course of the Orinoco during the Cenozoic (Rod 1981; Díaz de Gamero 1996) would predict the discovery of Early Miocene freshwater forms in Lara state. Relevant to this are some of the fossils from the Cerro La Cruz fauna. In addition to nearshore marine elements, the Castillo Formation fauna contains freshwater cachama fish and croakers (Aguilera and Rodrigues de Aguilera 2004b; Dahdul 2004; Aguilera and Lundberg this volume), represented by

Table 3.1. Fossil Vertebrates Reported from the Cerro La Cruz and Siquisique Localities of the Castillo Formation, Lara State, Venezuela (Sánchez-Villagra et al. 2000, 2001, 2004)

Elasmobranchii
- Hemigaleidae, *Hemipristis serra*
- Carcharhinidae, *Carcharhinus* cf. *obscurus, Carcharhinus cf. perezi Carcharhinus falciformis*
- Squalidae ? indet.
- Myliobatidae, *Rhinoptera* sp.

Teleostei
- Sphyraenidae, *Sphyraena* sp.
- Scombridae, *Acanthocybium* sp.
- Sciaenidae, *Protosciaena neritica*
- Ariidae, cf *'Arius,'* cf *'Bagre'*
- Characidae, *Colossoma macropomum, Mylossoma* sp.

Testudines
- Podocnemididae, *Bairdemys* sp.
- Trionychoidea indet.

Crocodylia
- Gavialoidea, *Siquisiquesuchus venezuelensis*

Mammalia
- Cetartiodactyla, Iniidae Gen. et sp. indet., Platanistoidea indet., "Squalodontid" indet., aff. *Prosqualodon australis*

Xenarthra, Tardigrada indet.
Sirenia indet.
Astrapotheria, Astrapotheriinae indet A., Astrapotheriinae indet B.

either isolated teeth or otoliths, and a sirenian represented by isolated ribs (Sánchez-Villagra et al. 2004). These taxa clearly indicate hydrographic relationships that do not exist today.

The main paleontological work on the Castillo Formation (Sánchez-Villagra and Clack 2004) has concerned exposures in Lara state. According to Wheeler (1963), the exposures of the Castillo Formation in Falcón state are of Oligocene age. Ample exposures are found in the western part of the state. A short expedition we led in 2004 resulted in the discovery of the first continental vertebrates from this formation in this area. Fragmentary turtle and crocodile remains were found approximately 2 km northwest of the town of Bariro and also on the road to "Los Chuchos," east of Dabajuro. All the fossils were found on the surface, in one case embedded in hard sandstone (Sánchez-Villagra et al. 2004).

Proticia venezuelensis was described by Patterson (1977) as the oldest fossil mammal from Venezuela, with a stratigraphic occurrence reportedly in the Eocene rocks from the Trujillo Formation. But *P. venezuelensis* was found in the southern flank of the Serranía La Baragua, Lara state, an area with extensive exposures of the Castillo Formation, from which this fossil may actually originate (Sánchez-Villagra et al. 2000). *Proticia venezuelensis* was described by Patterson (1977) as a representative of the Pyrotheria, an extinct order of ungulate-like mammals of uncertain affinities (McKenna 1980; Lucas 1986). A cuspate tooth form, the presence of thick enamel, and the paleoenvironmental context call into question

the purported taxonomic identification and make the possibility of sirenian affinities worth considering (Sánchez-Villagra et al. 2000; Bond and Gelfo this volume).

Quiamare Formation, Río Guere Site, Early–Middle Miocene

Simpson (1947) described the glyptodontid *Asterostemma venezuelensis* based on an incomplete carapace and a mandibular fragment, which has been placed in the new genus *Boreostemma* (Carlini and Zurita this volume).

The fossil described by Simpson (1947) is reported to come from the banks of the Guere River, close to the town of San Francisco, about 40 km SW of Barcelona in Anzoátegui state. The exact layer in which the fossil was found is unknown, and the only indication we have as to its stratigraphic provenance is that it is from the "middle Miocene" since it comes from the "Santa Inés Formation." This formation is no longer considered valid (Ministerio de Energía y Minas 1997). Exploration of the area and consideration of all available information on the geology of the area leaves no doubt that the fossil was collected in the Salomón Member of the Quiamare Formation. The mollusk fauna reported from this member suggests a late Middle Miocene to early Late Miocene age (Vivas and Macsotay 1989).

Only few exposures of the Quiamare Formation are known, where roads are being built or where the river cuts into sediments in the area around the town of San Francisco, which is mostly covered by vegetation. A site of easy access is located on the eastern side of the bridge over the Guere River, 1.5 km from the town of San Francisco, but it is not fossiliferous.

Chaguaramas Formation, Quebrada Honda Site, Early or Middle Miocene

The Chaguaramas Formation fauna includes several remains of mammals, crocodiles, and turtle shells, studied in part by Stehlin (1928) and Simpson (1943). Outcrops are located in an area of the Quebrada Honda, about 10 km northwest of Zaraza, Guárico state. Fossils were found in a sandy matrix, assignable to the upper member of the Chaguaramas Formation, which is considered to be Middle Miocene (González de Juana, Iturralde de Arozena, and Picard 1980: 622–23) or, based on more recent studies, Early Miocene (Macsotay and Wesselingh 2005) age. The upper member containing fossil vertebrates comprises alternating shales and sandstones, in which lignite or carbonaceous shale beds are common. Mottled clay beds suggest subaerial oxidation, and a complete emersion of the topmost horizons, which were probably deposited in a savanna environment (Macsotay and Wesselingh 2005).

The first vertebrate described for this locality was the astrapothere *Astrapotherium christi* (Stehlin 1928), based on an almost complete lower jaw, today in the collections of the Naturhistorisches Museum in Basel. This material was referred soon after to the genus *Xenastrapotherium*

by Kraglievich (1928). Cabrera (1929) described a year later *Xenastrapotherium kraglievichi* from La Venta in Colombia. An incomplete and edentulous skull from the Eastern Cordillera in Bolivia was assigned tentatively by Hoffstetter (1977) and by Frailey (1987) to the genus *Xenastrapotherium*. According to MacFadden et al. (1990) the rocks containing this fossil are of an absolute age between 13.0 and 12.7 Ma, based on paleomagnetic and isotopic data.

The second vertebrate reported for this fauna is the pleurodire described by Simpson (1943) as *Podocnemis geologorum*, based on an incomplete carapace and a plastron (Sánchez-Villagra and Scheyer, this volume). The other vertebrates collected in Quebrada Honda were indeterminate fragments of crocodiles and turtles, and might be at the Naturhistorisches Museum in Basel, where Dr. Peter Christ sent them for study (Stehlin 1928). It is likely that some other fragmentary reptile remains from this locality, collected by G. G. Simpson, are deposited at the American Museum of Natural History (AMNH) in New York.

Río Yuca and Parangula Formations

Significant fossil vertebrates have been collected from deposits in Portuguesa and Barinas states, which correspond to one or two geological units reportedly deposited in deltaic environments (González de Juana, Iturralde de Arozena, and Picard 1980; Ministerio de Energía y Minas 1997). The "Léxico Estratigráfico de Venezuela" (LEV, Ministerio de Energía y Minas 1997) assigned a Late Miocene–Pliocene age to the Río Yuca Formation, based on its stratigraphic position, but did not provide any further information on this matter. According to the LEV the Río Yuca Formation represents continental deposits, with typically green sediments. Most of the Parángula Formation is characterized in contrast by yellow or red sediments (Campos 1977; Ministerio de Energía y Minas 1997). Abundant palynomorphs clearly indicate a principally lower Miocene age for Parángula, possibly reaching the Oligocene in some areas (Ministerio de Energía y Minas 1997). Kiser (1997 in Ministerio de Energía y Minas 1997) suggested a Late Oligocene–Middle Miocene age for the Parángula Formation in the subsurface of Barinas. The LEV gives an Early–Middle Miocene age for Parángula. The geology of the Río Yuca and Parángula formations was described in an unpublished report (M. S. Osuna 1994, CORPOVEN) according to the Ministerio de Energía y Minas (1997). Their age is in the Middle Miocene, with Río Yuca Formation being on top and therefore younger.

Aguasuelos (1990, in Ministerio de Energía y Minas 1997) reported from the Río Yuca Formation the presence of angiosperm leaves, a rodent molar, and bones of a large mammal. Aguasuelos (ibid.) also mentioned the presence of bones belonging to small mammals, turtles, and Crocodylia from the Parángula Formation, although O. Macsotay (pers. comm. to MRSV 2006) suggested that the rocks containing these fossils belong to the Río Yuca Formation.

A few remains of a megatherid were described by Collins (1934) as *Prepotherium venezuelanum*, from the barrancas of Tucupido River, about 7 km northwest of the town of Tucupido, Portuguesa state. This fossil was originally assigned to the base of Río Yuca Formation, but Rondón (in Stephan 1977) and Aguasuelos (1990, in Ministerio de Energía y Minas 1997) pointed out that the discovery site corresponds to the underlying Parángula Formation. The geologist Heroy of the Sinclair Exploration Company collected the fossil in a layer containing red limestone and sandstones (Collins 1934), colors characteristic of Parángula Formation sediments. Hoffstetter (1961) suggested a new genus *Pseudoprepotherium* to accommodate this fossil, a taxonomic change accepted by xenarthran workers (Hirschfeld 1985; McDonald 1997; Carlini, Scillato-Yané, and Sánchez 2006). The same genus has been reported from the Middle Miocene of La Venta (Hirschfeld 1985), and the Late Miocene–Pliocene of Acre (Bocquentin Villanueva and Guilherme 1999), and thus seems to have been restricted to tropical regions.

Aguasuelos (1990, in Ministerio de Energía y Minas 1997) described the strata in which Collins (*fide* Pierce 1960) found *Prepotherium venezuelanum* as a fluvial channel with cross-bedding, associated with a sequence of paleosols with layers of sandstones and conglomerates, which belong to the upper portion of the Parángula Formation and not the basal ones of Río Yuca.

Approximately 20 km northeast of the site from which Collins (1934) described its megatherid, O. Macsotay and colleagues (pers. comm. to MRSV January 2006) found cranial and postcranial remains of a sirenid in sediments belonging to the Río Yuca Formation.

A sebecid crocodile was found in Quebrada La Yuca, a tributary of the Socó River, near the Barrancas de Barinas, in Barinas state. This fossil, from the Parángula Formation, represents the first sebecid report for Venezuela and indicates continental deposits for the locality. The fossil consists of the rostral portion of the skull and the anterior half of the lower jaw. It was embedded in a medium- to coarse-grained sandstone. The fossil belongs to the collection of the Museo Alberto Arvelo Torrealba of Barinas City and was brought to the Museo de Ciencias Naturales of the Universidad Simón Bolívar by MRSV in 1992 for study. Based on this material, Paolillo and Linares (2007) described a new genus and species *Barinasuchus arveloi* and assigned to it Peruvian material from the Ipururo Formation in the upper basin of the Ucayali River formerly referred to *Sebecus* cf. *huilensis* (Buffetaut and Hoffstetter 1977). This species had been first described from the Middle Miocene deposits of La Venta in Colombia. As is the case with other sebecosuchian crocodiles, the Venezuelan specimen shows remarkable convergences in tooth morphology and overall cranial shape with carnivorous dinosaurs and some extinct crocodyliforms from the Mesozoic (Gasparini, Pol, and Spalletti 2006), with an appearance quite uncharacteristic of living crocodiles (Buffetaut 1980; Gasparini, Fernández, and Powell 1993). No postcranial

Table 3.2. Vertebrate Faunal List for the Urumaco Sequence
(Socorro, Urumaco, and Codore Formations)

Chondrichthyes
Lamnidae Megaselachus megalodon
Hemigaleidae *Hemipristis serra*
Carcharhinidae Carcharhinus sp., Galeocerdo cuvier, Negaprion eurybathrodon, Rhyzoprionodon sp.
Pristidae Pristis aff. pectinata
Dasyatidae *Dasyatis* sp.
Myliobatidae Aetobatus arcuatus, Myliobatis sp., Pteromylaeus sp., Rhinoptera sp.
Rhinobatidae Rhynchobatus sp.

Osteichthyes
Pimelodidae Phractocephalus nassi, Platysilurus sp.
Loricariidae Acanthicus sp.
Doradidae Doras dionae, Doraops cf. zuloagai, Rhinodoras cf. thomersoni
Ariidae Amphiarius rugispinis, Aspistor quadriscutis, Bagre marinus, Notarius kessleri, Sciades couma, S. dowii, S. herzbergii, S. troscheli
Serrssalmidae Piaractus sp.
Erythrinidae indet.
Scianidae Cynoscion sp., Equetus sp., Larimus henrii, L. steurbauti, Micropogonias coatesi, Ophioscion lundbergi, Pachyurus jungi, Plagioscion urumacoensis
Haemilidae Haemulon sp.
Serranidae Epinephelus itajara

Sauropsida
Aves, Ciconiformes, Ciconiidae Jaribu codorensis
Aves indet.
Crocodylomorpha
Alligatoridae Caiman brevirostris, Caiman lutescens, Melanosuchus fisheri, Purussaurus mirandai
Crocodylidae Thecachampsa sp.
Gavialidae Brasilosuchus mendesi, Grypossuchus jessei, Grypossuchus croazati, Hesperogavialis cruxenti, Ikanogavialis gameroi
Nettosuchidae Mourasuchus arendsi
Squamata, Ophidia
Aniliidae Colombophis cf. C. portai
Boidae, Boinae Gen. et sp. indet.
Alethinophidia Gen. et sp. indet.
Testudines
Podocnemididae Bairdemys venezuelensis, Bairdemys sanchezi, Bairdemys winkleri, Stupendemys geographicus
Trionychidae indet.
Chelidae Chelus lewisi

Mammalia
*Marsupialia, Borhyaenidae indet.
Cetacea, Odontocete indet.1; Odontocete indet.2
Xenarthra
Megatheriidae Urumaquia robusta, Proeremotherium eljebe
Megalonychidae Pronothrotherium sp. New genus and species
Mylodontoidea Urumacotherium garciai, Mirandabradys socorrensis, Mirandabradys urumaquensis, Mirandabradys zabasi, Bolivartherium urumaquensis, Bolivartherium codorensis
Glyptodontidae Boreostemma pliocena
Sirenia, Dugongidae *Nanosiren sanchezi,* ?*Metaxytherium*
Sirenia indet.
Litopterna, Protherotheriidae, Megadolodinae *Bounodus enigmaticus*

Notoungulata
*Typotheria Interatheriidae indet.
*Hegetotheria Hegetotheriidae indet.
Toxodontidae indet.
Astrapotheria indet
Rodentia. Caviomorpha
Phoberomys pattersoni, cf. Potamarchus, *Eumegamys sp., *Tetrastylus sp., *Kiyutherium octolaminatus, *?Cardiatherium sp.

Source: Mostly based on a summary by Sánchez-Villagra and Aguilera (2006), who present a complete list of references. Updates based on Sabaj Pérez, Aguilera, and Lundberg (2007), Lundberg et al. (in press), Riff and Aguilera (2008), and Domning and Aguilera (2008) and on unpublished discoveries made by the authors and collaborators in the last few years. Taxa marked by an asterisk were reported by Linares (2004b), but we have not been able to check those reports.

remains, an area of the anatomy poorly known in this group, are known for this species.

Urumaco Sequence: Socorro, Urumaco, and Codore Formations

The geology of the Urumaco sequence (Middle Miocene–Pliocene) is treated by Quiroz and Jaramillo (this volume), and several aspects of its fauna are discussed in other chapters: rodents (Horovitz et al.), xenarthrans (Carlini and Zurita), crocodiles (Scheyer and Moreno), turtles (Sánchez-Villagra and Scheyer), fishes (Aguilera and Lundberg), and decapods (Aguilera et al.). Aguilera (2004) presented a synthetic work on the fauna, Sánchez-Villagra and Aguilera (2006) an overview of it, and Cozzuol (2006) a comparison of the most diverse northern neotropical fossil vertebrate areas, including Urumaco. In table 3.2 we present the vertebrate faunal list updated with discoveries of the last few years, which include postcranial material (AMU-CURS-177; Lower Member of the Urumaco Formation; coordinates: 363266/1237350) of a second bird species to that reported by Walsh and Sánchez (2008), a sirenian skull (fig. 3.2), a dolphin dentary, and a large cetacean humerus, among other taxa (figs. 3.3, 3.4). Our ongoing work in the San Gregorio Formation promises to provide a view of another diverse fauna in the Urumaco sequence, this time of Pliocene age and preserving some microvertebrates, otherwise rare in this area.

Work on fossil vertebrates from Urumaco until now has been mostly taxonomic and in some cases phylogenetic; little has been done or discussed specifically on the adaptations or paleoecology of these animals (Aguilera 2004; Scheyer and Sánchez-Villagra 2007). Perhaps isotope analyses and the integration of stratigraphical and paleoenvironmental data can be used in future paleobiological studies of the Urumaco sequence fauna. A diversity of coprolites of different kinds and sizes from many localities of the Urumaco sequence (fig. 3.5) could also become informative in paleoecological studies.

Fig. 3.2. *top* An undescribed sirenian from the Urumaco Formation, El Mamón locality, in the collections of the Universidad Simón Bolívar, Caracas. *Photo by M. R. Sánchez-Villagra. Scale bar = 10 cm.*

Fig. 3.3. *bottom* Restoration of a dugong from Urumaco. Fossils of sirenians are rare in the Urumaco sequence, although rib fragments are found at several localities. *Artwork by Jorge González.*

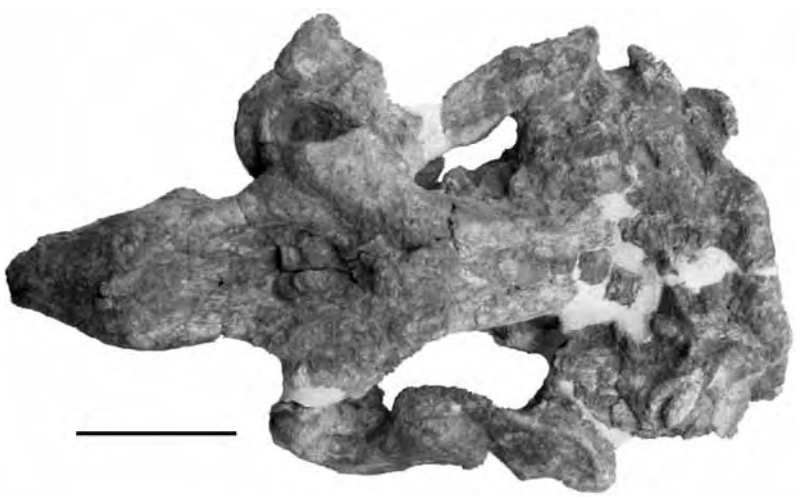


Fig. 3.4. *following page, top* Only isolated dentaries of dolphins are known from the Urumaco sequence. The restoration depicted here is highly speculative, although animals similar to these undoubtedly inhabited Urumaco in the Late Miocene. *Artwork by Jorge González.*

Cantaure Formation

Nolf and Aguilera (1998, see also Aguilera and Rodrigues de Aguilera 2001, 2004a) described a diverse fish fauna from the Cantaure Formation, including sixty-one taxa, mostly identified at the generic or specific level. These studies included the description of nine new species. According to Nolf and Aguilera (1998), the Early Miocene Cantaure Formation fauna reflects a complex and stable neritic littoral ecosystem. From the same formation and localities, Jung (1965) and Aguilera et al. (this volume) described diverse faunas of mollusks and decapods, respectively. The evidence presented by these authors is in agreement with the stable and productive shallow-water and intertidal paleoenvironments also suggested by the fish fauna.

Fig. 3.5. Coprolites from the Urumaco Formation. Scale bar = 5 cm.

Cumaca Formation, Tuy Basin, Middle Miocene

Bermúdez (1966) reported fish scales and teeth, and M. R. Sánchez-Villagra (unpublished) found unidentified fish otoliths and teeth associated with the freshwater gastropod *Tryonia* from the Cumaca Formation. From the same locality, Macsotay et al. (Macsotay, Peraza, and Wehrmann 1995, Macsotay et al. 1995) reported the presence of coprolites, crocodile teeth, turtle carapace fragments, and a small rodent molariform tooth assigned to *Prolagostomus* sp. (Chinchillidae), based on a preliminary identification by J. L. Hartenberger. Horovitz et al. (this volume) have determined that the tooth is that of a dinomyid. The fossiliferous exposures are located on the road Caucagua–Araguita, Miranda state, in the western margin of the Tuy basin. The vertebrate fossils were found in green limestone, sediments with a dip of 32° southeast. Freshwater gastropods from the same locality were studied by Wesselingh and Macsotay (2006). As discussed by these authors and by Macsotay et al. (Macsotay, Peraza, and Wehrmann 1995, Macsotay et al. 1995), the Cumaca Formation contains freshwater deposits of Middle Miocene age. According to Wesselingh and Macsotay (2006, 65) the occurrence of the mollusk *Tryonia* in the Cumaca Formation indicates a closer biogeographic affinity of northern Venezuela and western Amazonian faunas during the Middle Miocene.

Work at the brick factory (Alfarería Caribe) located at the site where the fossils have been recovered has meant that much of the exposed Cumaca Formation in this area has been lost. In another quarry of this company in a nearby exposure (10° 15' 20.4" N, 66° 25' 57.6" W) 2 km away from the main site at Alfarería Caribe, the proximal humerus of a Megatheriinae was found and kindly provided for study to us. We report on this fossil here for the first time (fig. 3.6). The humeral diaphysis has a subtrapezoidal outline, similar to that of *Pyramiodontherium brevirostrum* (Carlini et al. 2002) with the anterior (largest) face slightly convex centrally. The humeral tuberosities form an angle of about 115° between

Fig. 3.6. Proximal humerus of a Megatheriinae (UNEFM-uncatalogued) from the Cumaca Formation, middle Miocene of Miranda state, Venezuela. Scale bar = 5 cm.

them, similar to the condition in *P. brevirostrum*, much more obtuse than that in *Pyramiodontherium scillatoyanei* (De Iuliis, Ré, and Vizcaino 2004), and the proximal articular surface has an almost circular outline. The shape and size are similar to those of *Pyramiodontherium* species from the "Araucarian" (late Miocene–Pliocene) of Argentina (see Carlini et al. 2002, figs. 3 and 4; De Iuliis, Ré, and Vizcaino 2004).

Capadare Formation, Middle Miocene

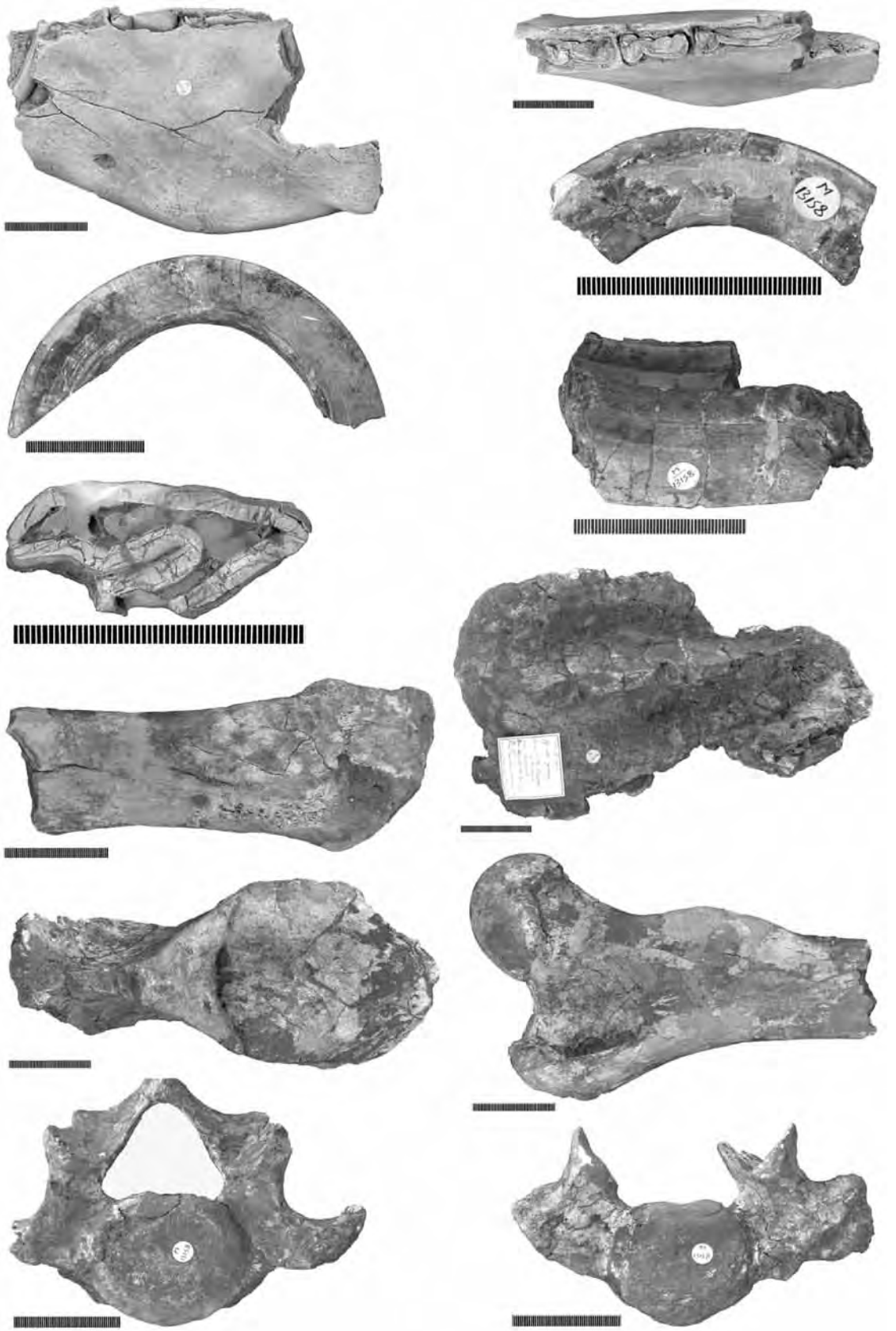
The first vertebrate record from the Capadare Formation was that of Rincón and Stucchi (2003), a fossil bird from a Middle Miocene limestone exposed in Cerro Misión, eastern Falcón state. The specimen comes from Cave of Zumbador and consists of a fragment of the anterior portion of the rostrum and was assigned to the Pelagornithidae (Pelecaniformes). According to Rincón and Stucchi (2003) the presence of this bird suggests a near-shore marine environment for eastern Falcón state during the Middle Miocene.

La Puerta Formation, Late Miocene

Young (1960) mentioned the presence of fish remains in the upper portion of the La Puerta Formation (Timoteo Member), which is characterized by the presence of red limestone. The Ministerio de Energía y Minas (1997) suggested a Late Miocene age for this formation.

Gyrinodon quassus was described by Hopwood (1928), from west of Buchivacoa in western Falcón state, Venezuela (see also Van Frank 1957). The holotype of *Gyrinodon quassus*, BMNH 13158 (formerly BMGD), is a left mandibular ramus with only the roots of m1–m3. Together with the mandibular ramus, and presumably from the same individual, are isolated upper teeth including right I2, P2, P3, M1? and M3, and left P4 and M2?, skull cap, and miscellaneous postcranial elements (fig. 3.7). Paula Couto (1982), and Bocquentin Villanueva and Silva (1994) referred isolated lower molars from Acre province (Brazil) to *Gyrinodon*. Nasif, Musalem, and Cerdeño (2000) mentioned the presence of *Gyrinodon* in Bolivia in addition to its occurrences in Venezuela and Brazil. The existence of material of *Gyrinodon* from the Urumaco Formation has been recorded by Linares (2004a), an assignment contested by Bond, Madden, and Carlini (2006). Madden (1997) included *Gyrinodon* together with *Pericotoxodon* Madden, 1997, and *Dinotoxodon* Mercerat, 1895, in a new subfamily of advanced Toxodontidae, the Dinotoxodontinae, on the basis of dental characters and presumably unique mandibular morphology. However, with the discovery and description of *Hoffstetterius imperator* Saint-Andre, 1993, from Bolivia, Saint-Andre (1993) could not confirm the validity of the "Dinotoxodontinae" (see also Nasif, Musalem, and Cerdeño 2000). Among the original material of *G. quassus* are upper teeth the morphology of which was never adequately described and yet is critical for the taxonomic assessment of material subsequently referred to *Gyrinodon* by other workers, including material from Acre in Brazil (Paula Couto 1982; and UFAC 1292 and 1417 by Bocquentin Villanueva

Fig. 3.7. *Gyrinodon quassus,* BMNH 13158. Cranial and postcranial remains. Scale bars = 50 mm.



and Silva 1994). As discussed by Sánchez-Villagra and Scheyer (this volume), Swinton (1928) presented a short note about the occurrence of four reptilian remains associated with the remains *Gyrinodon quassus*. Besides a crocodile vertebra, three fragments of a turtle carapace were mentioned.

Las Piedras Formation, Upper Miocene–Pliocene

Hedberg et al. (1947, in Odreman Rivas and Medina 1984, 73) reported the presence of fishes from the area of Oficina, Anzoátegui state. Funkhoser et al. (1948, in Odreman and Medina 1984, 73) mentioned a horizon with turtles in the area of Anaco, Anzoátegui state. This formation is exposed in Monagas and Anzoátegui states. According to Hedberg (1950), the paleoenvironment was a lowland with freshwater to brackish waters influence.

Guamacire Formation: Middle Miocene or Upper Miocene–Pliocene

The anterior portion of a cetacean skull was reported by Odreman and Medina (1984, 74, see also Ministerio de Energía y Minas 1997) from the Quebrada El Abra, around El Tocuyo, Lara state. The material was reported by these authors to be deposited at the Escuela de Geología of the Universidad Central de Venezuela in Caracas. This fossil was collected by J. Royo y Gómez, who identified it as a "new Pleistocene mammal." Studies of the sediments found in between the teeth of this fossil revealed the presence of the foraminifera *Globorotalia fohsi*, which indicates a Miocene age (Odreman and Medina 1984). Because of the characteristics of the associated sediments and its geographic provenance, Odreman and Medina (1984, 74) suggested that the fossil may come from the Guamacire Formation.

Based on previous reports of ostracods and foraminiferan species, the Ministerio de Energía y Minas (1997) reported a Middle Miocene age for this Formation. Odreman and Medina (1984) reported instead an Upper Miocene–Pliocene age. According to the Ministerio de Energía y Minas (1997), the Guamacire Formation preserves coastal lagoon paleoenvironments, influenced by continental sedimentation. Ministerio de Energía y Minas (1997) incorrectly pointed out that finding a cetacean implies a deep-sea paleoenvironment, because the cetacean record reflects outer neritic environments. There it was also suggested that the formation indicates a gradient ranging from marginal marine environment to lagoonal and continental.

Cubagua Formation, Pliocene

The Cubagua Formation contains sediments from the Late Miocene to Early Pliocene and is exposed along the Araya Península, Cubagua Island, Margarita Island, and the northern Paria Península (Aguilera and Rodrigues de Aguilera 2001). This formation is divided into four formal members: the Cerro Verde Member, exposed on Cubagua Island and the westernmost Araya Península; the Cerro Negro Member, exposed

along the western Araya Península and Cubagua Island; and the La Tejita and Las Hernández members, exposed on Margarita Island. Macsotay, Peraza, and Wehrmann (1995) presented an alternative arrangement, defining a Cubagua Group, giving the status of formation to the members, and discussing details of the geology of these sediments.

Aguilera and Rodrigues de Aguilera (2001) described several fish faunules from the Cubagua Formation, represented mostly by teeth and otoliths. In total these authors reported 140 species in 115 genera and 63 families of elasmobranch and teleost fishes. They described the lanternfish species *Lampadena jacksoni* (Myctophidae) based on otoliths. According to Aguilera and Rodrigues de Aguilera (2001), the depositional depth based on fish fauna association suggests an inner neritic environment under coastal upwelling conditions.

Aguilera and Rodrigues de Aguilera (2004a) also reported on the giant-toothed white shark *Carcharodon megalodon* (=*Megaselachus megalodon*) and the wide-toothed mako *Isurus xiphodon* (=*Cosmopolitodus hastalis*) from this formation. Head, Sánchez-Villagra, and Aguilera (2006a) reported a trionychid turtle from this formation, from a locality on Margarita Island, at the Santiago Mariño International Airport (see Sánchez-Villagra and Scheyer this volume).

Paraguaná Formation

Rodriguez (1968), and Aguilera and Rodrigues de Aguilera (2004a) reported giant-toothed white sharks *Carcharodon megalodon* (=*Megaselachus megalodon*) from the Amuay Member of the lower Pliocene Paraguaná Formation. There is a rich fauna of mollusks and foraminifera from this formation, which is thought to be of Early Pliocene age (Ministerio de Energía y Minas 1997).

Tuy Formation: Pliocene–Pleistocene

Bermúdez (1966) reported that the Tuy Formation in Miranda state contains faunas typical of freshwater lagoons, including fish teeth, scales, and spines. Picard and Pimentel (1968) also mentioned scales, teeth, and fish scutes. Odreman and Medina (1984, 74) also cited Macsotay (1968) as a source of a report of fossil fishes from this locality. Macsotay (pers. comm. to MRSV January 2006) reported the finding of teeth and isolated vertebrate bones from exposures of this formation near the crossing of the highway to eastern Venezuela with the road leading to Ocumare del Tuy, Miranda state.

The Ministerio de Energía y Minas (1997) suggested a Pliocene–Pleistocene age based on the work of Beck (1985) on ostracods from the underlying Siquire Formation (of Late Miocene–Pliocene age) and of González de Juana, Iturralde de Arozena, and Picard (1980) based on sedimentology. But previous authors had suggested a Late Miocene–Pliocene age (Bermúdez 1966; Macsotay 1968; Picard and Pimentel 1968), the age reported by Odreman and Medina (1984).

Late Pleistocene Sites of TaimaTaima, Muaco, Quebrada Ocando, and Cucuruchú

During the Quaternary important climatic changes took place in Venezuela that undoubtedly influenced the evolution of the fauna and flora in this country (Rull et al. this volume). Some areas of Venezuela are rich in vertebrate fossils that document local or more global extinctions, biotic alterations associated with climatic changes, and, in some cases, even the arrival of humans in the Americas. The Late Pleistocene sites of Muaco, TaimaTaima, Quebrada Ocando, and Cucuruchú, all from the Municipio Colina, Falcón state, contain archaeological remains as well as fossils (Bocquentin Villanueva 1979, 1982; table 3.3). At some sites stone artifacts have been found that can be related to hunting the associated megafauna. These sites have in common the proximity of water wells, known locally as *ojos de agua* or *pozos.* It has been speculated that animals went to drink from these water wells, and it is in these sites where humans hunted the megafauna (Aguilera 2006).

Table 3.3. Faunal List for the Quaternary Sites of Northeastern Falcón State according to Aguilera (2006) and Soibelzón and Rincón (2007)

Xenarthra, Phyllophaga: Megatheriidae (giant sloths): *Eremotherium laurillardi;* Mylodontidae (giant sloths): *Glossotherium tropicorum*
Xenarthra, Cingulata: Glyptodontidae (giant armadillos): *Glyptotherium* sp.; Pampatheriidae (giant armadillos): *Pampatherium* sp., *Holmesina* sp.
Carnivora: Ursidae (short-faced bears): *Arctotherium wingei;* Canidae (wolves): *Canis dirus;* Felidae (jaguars): *Panthera (Jaguarius) onca;* Mephitidae (skunks): *Conepatus* cf. *semistriatus*
Notoungulata: Toxodontidae (South American "hippos"): *Mixotoxodon larensis*
Litopterna: Macrauchenidae (false camelids): *Xenorhinotherium bahiense*
Proboscidea: *Gomphotheridae (mastodonts): *Stegomastodon waringi*
Perissodactyla: Equidae (horses): *Equus* (*Amerhippus*) *neogeus*
Artiodactyla: Camelidae (llamas, guanacos, vicuñas): *Palaeolama major;* Cervidae (deer): *Odocoileus salinae; Mazama* sp.
Testudines: Testudinidae (tortoises): *Geochelone* (*Chelonoidis*) sp.
Ophidia: Viperidae (viper snakes): Gen. et spec. indet.

TaimaTaima

This site is located 2.5 km northwest of the town of TaraTara (11° 29' 57" N, 69° 31' 18" W). The sediments are gray fine-grained sandstones in strata 0.75–1 m wide, lying on top of Miocene sandstones of the Caujarao Formation. The area of TaimaTaima is semi-arid, with an annual rainfall rarely exceeding 300 mm with the annual maximum temperature reaching around 38 °C. The vegetation is xerophytic. The age of the fossil-bearing unit of sediments (Bryan et al. 1978) was established using ^{14}C dating on several samples. Tamers (1971) dated bones and sediment samples and estimated an age between 14 ka and 12 ka years before present. Gruhn and Bryan (1984), based on the study of plant remains, provided a date between 12.580 (±150) ka and 13.390 (± 130) ka BP.

Muaco

This site is located in the town of Muaco (11° 28' 51" North, 69° 32' 41" West). It consists of a 2–3 m thick layer of lime sediments overlying Miocene sandstones of the Caujarao Formation. The age of the fossil bearing

sediments was estimated at 14.300 (±500) and 16.375 (± 400) ka (Royo y Gómez 1960b; Rouse and Cruxent 1963; Ochsenius 1980). The mammals in the Muaco assemblage indicate open savanna/forested savanna paleoenvironments (Bocquentin Villanueva 1979). The stratigraphic levels with fossils are usually limestones, which form paleosols. Discovery of fossils from El Muaco dates back to the 1950s, when a school teacher at the Liceo de Coro, F. Gutiérrez, was contacted by local farmers and explored some areas. These discoveries stimulated the interest of J. M. Cruxent and J. Royo y Gómez (Royo y Gómez 1960a, 1960b; Cruxent 1967, 1970). After the death of Royo y Gómez in 1961, Cruxent continued the work, in many cases in collaboration with other researchers (Bocquentin Villanueva 1982; Bryan et al. 1978; Gruhn and Bryan 1984).

Of particular interest in the Muaco fauna is the reported fossil short-faced bear *Arctotherium wingei*, also occurring in the Cueva del Guácharo in northeastern Venezuela (Soibelzón and Rincón 2007). The first Venezuelan record of fossil Tremarctinae was made by Royo y Gómez (1960 a, 1960b). It is potentially significant that of the five recognized species of *Arctotherium*, Soibelzón and Rincón (2007) suggested the presence of *A. wingei* in Venezuela. The age of the deposits containing it is Late Pleistocene, while the other *Arctotherium* species are reported from older Pleistocene deposits from more southern localities than those in Venezuela. Soibelzón and Rincón (2007) suggested that *A. wingei* is a basal species in the genus. Possibly this fossil bear presents an example of a basal species that persisted in the tropics while being otherwise extinct at higher latitudes (Carlini, Vizcaíno, and Scillato-Yané 1997; Carlini, Scillato-Yané, and Sánchez 2006; Carlini and Zurita this volume). Additionally, Carlini, Zurita, and Aguilera (2008) reported for the first time the genus *Glyptotherium* from South America, based on the study of specimens from TaimaTaima, Muaco, Quebrada Ocando, and Cucuruchú, which had been originally assigned to *Glyptodon*.

Chávez-Aponte, Alfonzo-Hernández, and Carrillo-Briceño (2008) recently revised the dental remains of the proboscidean gomphotheres from Muaco and found much variability in the sample. They concluded that it is not possible at the moment to provide a generic affiliation for these materials.

Cucuruchú

Cucuruchú is located about 10–15 km east of Coro and 2 km northeast of TaraTara. It is in a small hill close to the Arroyo de Cucuruchú, in the Municipio Colina of Falcón state, about 200 m from the coast (11° 30' 10" N, 69° 30' 17" W). The site consists of a thin layer of reworked limestone fragments of variable large sizes embedded in a limestone matrix. This layer of fluvial origin ranges in thickness from a few centimeters up to a meter and a half, and it is the main fossil-bearing layer. Over this layer there is a gray/brown limestone containing traces of plant stems and leaves. It is presently 10 m thick but originally was thicker and most likely of lacustrine origin. Some fragmentary remains of vertebrate fossils have

been found in the lowest part of this limestone layer (Cruxent 1970). The age of the fossil-bearing layer was estimated at 5.860 (±80) ka BP by Bryan (1973). This dating is not consistent with the fossil fauna found in the area (Aguilera 2006). The gravels at Cucuruchú (Bocquentin Villanueva 1982) record a large vertebrate fauna including turtles, snakes (Head, Sánchez-Villagra, and Aguilera 2006b), *Glyptotherium* sp., and *Equus* (*Amerhippis*) sp.

Head, Sánchez-Villagra, and Aguilera (2006b) reported an indeterminate viperid from the gravels at Cucuruchú, based on an isolated precloacal vertebra (UNEFM-CIAAP-1478). This occurrence of a viperid is consistent with the geologically young record of the lineage in South America. As discussed by Head, Sánchez-Villagra, and Aguilera (2006b), the geographical and temporal distribution of fossil snakes in Venezuela, in the context of the whole South American record, indicates independent dispersals of snakes into South America throughout the Neogene, as opposed to a single, larger biogeographic event.

Quebrada Ocando

The site is located in the valley formed by the Quebrada Ocando, southeast of the town of Mataruca (11° 25' 08" N, 69° 29' 47" W). A layer of reworked limestone fragments embedded in a fine sandstone matrix, of unknown absolute age, contains fossils.

Barquisimeto Local Fauna, Late Pleistocene–Holocene

In the Barquisimeto basin there are several paleontological sites. Paleontological exploration in this area started with the work of Nectario María, who produced reports and informal descriptions of the discoveries (e.g., 1938). The specimens collected were deposited at that time in the Colegio La Salle in Barquisimeto city. However, most of them deteriorated and were lost. G. G. Simpson (1939a, 1939b) explored the Barquisimeto area, finding near San Miguel a deposit rich in megatheres, mastodonts, and toxodonts.

In the area of Quíbor, Tocuyo, and Sanare there are more than twenty sites with isolated vertebrate remains. The main center where the collections are located is the Museo Arqueológico de Quíbor, and other specimens are in the Museo de Ciencias de Caracas.

The toxodont *Mixotoxodon larensis* was described by Van Frank (1957) based on several lower dental remains (fig. 3.8). The type material of *Mixotoxodon larensis* was collected near the town of San Miguel southwest of Barquisimeto, Lara state. Material referred by Van Frank (1957) to *Mixotoxodon larensis* includes specimens from Honduras (McGrew 1942) and El Salvador (Stirton and Gealey 1949; Webb and Perrigo 1984), and de Porta (1959) referred mandibular material from northern Colombia to the same species. Rincón (2007) interpreted morphological variation in the lower incisors of *Mixotoxodon larensis* as a case of intraspecific variation, possibly a case of sexual dimorphism.

Fig. 3.8. *opposite* Highly speculative restoration of *Mixotoxodon larensis*. *Artwork by Jorge González.*

Liddle (1928) mentioned remains of a large xenarthran and other Pleistocene mammal bones from strata at El Milagro, Zulia state.

El Milagro, Zulia State, Pleistocene

Mene de Inciarte Tar Pits

Natural asphalt seeps, also called "tar pits" or "menes," are found in northwestern Venezuela and were sought by geologists in the early part of the twentieth century as indicators of subsurface petroleum accumulations. The hydrocarbons in natural seeps ooze from the ground through porous rocks or geological faults and slowly cover patches of ground. Animals of all kinds and sizes become stuck in the tar, and some of them were not able to pull free. Places like this have produced fossil accumulations in a few parts of the world, including the famous Rancho La Brea in Los Angeles. These kinds of deposits are being exploited in Venezuela, with excellent results.

Work in the Mene de Inciarte was initiated by the geologist John Moody and colleagues in 1997. It is located in the Sierra de Perijá mountain front in northwestern Venezuela. The site is in the vicinity of the Río Cachirí and the village of Cachirí, northwest of the petroleum fields of La Paz. This singular site, located in a sparsely inhabited area easily

accessible in a few hours by car from Maracaibo city, is rich in animal diversity, and fossils are often very well preserved. Before this site was discovered, Quaternary small vertebrate fossils from Venezuela were unknown, other than discoveries from caves that are most likely of Holocene age (see below). A. Rincón has led work on the deposit, resulting in a series of publications by him and his associates, summarized below.

According to Rincón (2007), of the twenty-nine mammal species of Mene de Inciarte, twenty-one are new for the Late Pleistocene of Venezuela. He provided a list of taxa, which we include below with some additions (table 3.4). Remains of frogs, turtles, crocodiles, lizards, and snakes from this site are currently under study by A. Rincón and collaborators (e.g., Rincón, Alberdi, and Prado 2006).

Table 3.4. Mammalian Taxa from the Mene de Inciarte (based on Rincón, White, and McDonald 2008, with additions from other publications cited by A. Rincón in that text)

Rodentia: *Sigmodon hispidus, Calomys hummelinki, Holochilus sciureus, Heteromys anomalus, Proechimys* cf. *P. poliopus, Echimys* sp. Dactylomyinae gen et sp. indet., (Rincón 2008), *Calomys hummelincki, Holochilus sciureus,* cf. *Thomasomys,* Echimyidae n. gen. et sp., *Dasyprocta* sp., *Neochoerus* sp. (Rincón 2006b)

Chiroptera: *Lophostoma* cf. *L. silvicolum, Trachops cirrhosus,* cf. *Mycronycteris,* Phyllostomidae gen. et sp. indet., *Eptesicus fuscus,* Vespertilionidae gen. *et* sp. indet., and *Rhogeessa* sp.

Xenarthra, Cingulata: *Dasypus sabanicola, Propraopus sulcatus, Pampatherium humboldtii; Glyptodon clavipes*

Carnivora: *Protocyon troglodites, Urocyon cinereoargenteus, Smilodon populator* (Rincón 2006a)

Perissodactyla: *Equus* (*Amerhippus*) *santaeelenae* (Rincón, Alberdi, and Prado 2006)

Preliminary radiometric dating of Mene de Inciarte based on the study of samples from the two xenarthrans *Glyptodon* cf. *G. clavipes* and *Holmesina occidentalis*, resulted in an age estimate of 25–46 ka (Jull et al. 2004).

Because of the presence of species now extinct in the area in which Mene de Inciarte is located, it has been hypothesized that the environment was more humid in the past. According to Czaplewski, Rincón, and Morgan (2005, 777), it perhaps represented a "moist period just prior to the last glacial maximum (25 ka ago), or of a relatively long span of time sampling more than one climatic episode." To test this and to fully explore the extent of this new and important locality, a detailed chronology and further exploration of the Mene de Inciarte fossils would be worthwhile.

Czaplewski, Rincón, and Morgan (2005) reported on twenty-four bat fossil elements representing at least five genera in two families. This report included the first fossil record for *Rhogeessa*, as well as additional

Pleistocene records for *Lophostoma* cf. *L. silvicolum*, *Trachops cirrhosus*, cf. *Micronycteris* sp., and *Eptesicus fuscus*. The discovery of several bats characteristic of subhumid environments is relevant for the paleoenvironmental reconstruction.

Prevosti and Rincón (2007) reported on a canid assemblage from the Mene de Inciarte consisting of at least five species, with an age based on the assemblage's stratigraphical position in the dated site (Jull et al. 2004) of around 25–27 ka. Canids originated in North America, and the group expanded its distribution only in the Late Miocene. The record of the group in northern South America is very scarce; therefore this finding is significant. The fossils include the first record of the fox *Urocyon* from the Late Pleistocene of South America, and records of great geographical expansion for *Protocyon*. The fossils consist of isolated teeth and postcranial remains.

The Xenarthra from the Mene de Inciarte were studied by Rincón, White, and McDonald (2008). The assemblage includes the first reports for Venezuela of the following three taxa: *Dasypus sabanicola*, *Propraopus sulcatus*, and *Pampatherium humboldtii*, as well as a new record for *Glyptodon clavipes*. Rincón, White, and McDonald (2008) discussed the inclusion of some *Dasypus* species into the genus *Propraopus*. Cingulata from Mene de Inciarte form a heterogeneous faunal community dominated mainly by savanna elements, with some forest elements that could represent seasonally dry forest (ibid.).

Rincón (2006a) provided the first record of a saber-toothed cat from Venezuela. He reported *Smilodon populator* Lund, 1842 from not only the Inciarte tar pits, but also from Zumbador Cave in Falcón state (see below). The materials consist of a few isolated teeth and a metacarpal. Rincón determined the specific assignment based on a morphometric comparison with the different species recognized by Kurtén and Werderlin (1990). *Smilodon* was a large predator that has been reconstructed as having lived in savannas and wooded areas with substantial brushy undergrowth (Webb and Rancy 1996), which matches the reconstruction for the Inciarte tar pits based on other data.

Rincón, Alberdi, and Prado (2006) reported *Equus* (*Amerhippus*) *santaeelenae* (Spillmann) from Mene de Inciarte based on morphometric comparisons of dental remains with those of several species of the genus. Fossils also include several isolated postcranial remains. Like all other fossils from the Mene, they are deposited at the Museo de Biología of the Universidad del Zulia.

Lake Valencia

Lake Valencia is one of the very few large neotropical lakes situated at low altitude. It is reportedly one of the few lakes in South America from which long cores extending back to the Late Cenozoic may be obtained (Livingstone and van der Hammen 1978). There has been interest in the evolution of this lake and its associated fauna, and particularly during

the Pleistocene and the climatic changes that characterized this interval (Binford 1982). Confirmed or published reports of fossil vertebrates from the area are unknown to us; Berry (1939) reported the presence of remains of several fish and mammals but from historical or at the latest pre-Columbian times.

Pleistocene Mammals from Zumbador Cave

Rincón (2004) reported the following fossil mammals from Zumbador Cave, located 15.5 km south-southwest of Yaracal, Cerro Misión, Falcón state: *Eremotherium laurillardi*, *Holmesina* sp., Glyptatelinae gen. et sp. indet., *Neochoerus* sp., *Smilodon populator*, and *Mixotoxodon larensis*. Rincón (2006a) provided later details on *Smilodon* from that cave and argued that during the Late Pleistocene the area where Zumbador Cave is located was a savanna-type landscape with patches of dispersed trees.

Rincón and Stucchi (2003) reported a fossil bird belonging to the Pelagornithidae (Pelecaniformes) from the same Zumbador Cave but from the Middle Miocene Capadare Formation.

Subfossil Remains from Venezuelan Caves

There are numerous records of subfossil mammals from Venezuelan caves, and most of them are bats. As recently summarized by Czaplewski, Rincón, and Morgan (2005), the following records are known.

Cueva de Quebrada Honda, Aragua state: *Phyllostomus discolor*, *P. hastatus*, *Glossophaga soricina*, *Uroderma bilobatum*, *Platyrrhinus helleri*, *Chiroderma salvini*, *Artibeus cinereus*, *A. jamaicensis*, *Enchisthenes hartii*, *Sphaeronycteris toxophyllum*, *Desmodus rotundus*, *Eptesicus fuscus*, *Nyctinomops laticaudatus*, *Eumops perotis*, and *Molossus ater* (Linares 1968)

Cueva de Los Carraos, Miranda state: *Tadarida brasiliensis* (Linares 1969)

Cueva de La Brújula, Miranda state: *Desmodus rotundus* (Linares 1970)

Cueva del Guácharo, Monagas state: *Desmodus draculae* (Morgan, Linares, and Ray 1988)

Cueva Toromo, Zulia state: *Pteronotus parnellii*, *Pteronotus gymnonotus*, *Mormoops megalophylla*, *Chrotopterus auritus*, *Artibeus lituratus*, and *Natalus stramineus* (Rincón 1999)

Cueva del Cañón de Sorotamia, Zulia state: *Artibeus lituratus* (Rincón 1999)

Cueva de Los Murciélagos, Isla de Toas, Zulia state: *Leptonycteris curasoae* (Rincón 2001).

The bat *Lasiurus* sp. is also known from Cerro Pintado, Amazonas state (Linares unpublished, cited in Marshall et al. 1984). The most noteworthy report of a subfossil bat from Venezuela (Morgan, Linares, and Ray 1988; Ray, Linares, and Morgan 1988) is that of the fossil vampire bat *Desmodus draculae*, a species also known from five other sites ranging from Mexico to Brazil (Czaplewski, Krejca, and Miller 2003 and references therein). The species has not been dated for any of these sites, and

although it is typically assumed to be Late Pleistocene in age; according to Czaplewski, Krejca, and Miller (2003), "some indirect dates on materials associated with extinct vampire bones are relatively young."

Linares (1968) mentioned the presence of a cebid monkey in the Cueva de Quebrada Honda that may be assignable to *Cebus*. Considering the presence of extinct monkey species from other sites in South America (Hartwig and Cartelle 1996), the potential of Venezuelan caves once systematically explored for interesting discoveries of primates seems obvious.

Some discoveries of fossil or subfossil Pleistocene vertebrates in Venezuelan caves are discussed in other parts of this chapter, such as that of a short-faced bear from the Cueva del Guácharo, Monagas state (Soibelzón and Rincón 2007).

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Osteoderm morphology in recent and fossil euphractine xenarthrans

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Abstract

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The presence of osteoderms within the integument, forming a carapace, is one of the most distinctive features of armadillos with the external morphology of these elements forming the basis of most systematic schemes. This is especially true for fossil taxa, where these elements are most frequent in the palaeontological record. A detailed study of osteoderms from the cephalic shield and different regions of the dorsal armour of *Chaetophractus villosus* (Euphractinae, Xenarthra) was made and compared to those of the extant genus *Dasypus* (Dasypodinae, Xenarthra), and the extinct genus †*Eutatus*. Three distinct histological zones were recognized: outer and inner zones are thin, formed by regular compact bone, the middle zone is thicker, with large cavities that contain mainly adipose tissue, hair follicles, and sweat and sebaceous glands. The internal structure of †*Eutatus* (also a member of Euphractinae) osteoderms is close to that of *C. villosus*, consistent with the notion that these taxa are phylogenetically closely related. In contrast, *Dasypus* shows marked differences. *Dasypus* shows hair follicles associated with both gland types (sweat and sebaceous) and connected to foramina on the external surface. Although not observed in adult *C. villosus*, it has been documented during embryonic development, only to atrophy later in ontogeny. Furthermore, the presence of red bone marrow is rare in *C. villosus*, but widespread in *Dasypus novemcinctus* osteoderms. These results suggest an early split of both subfamilies and support the hypothesis that the Euphractinae are more derived than the Dasypodinae.

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Introduction

Armadillos (Cingulata, Dasypodidae) are the xenarthrans with the greatest temporal and geographical distribution. The oldest fossils date back to the early Tertiary [more than 50 million years ago (Ma)] of Brazil (Oliveira and Bergqvist 1998; Bergqvist *et al.* 2004), and their current distribution ranges approximately between 40°N and 40°S in the American continent. One of their most distinctive anatomical features is the presence of a protective dorsal cover (carapace) formed by osteoderms overlaid by epidermal horny scales. These osteoderms cover the head dorsally (cephalic shield) and the trunk (dorsal shield), and encase the tail (caudal sheath), except in the genus *Cabassous* ('naked tailed armadillo', Wetzel 1985). In addition, osteoderms may also be present within the integument above the rostrum, in the ventral surface of the trunk and in the limbs. However, these elements do not contribute to continuous shields in these areas and may not be associated with horny scales.

Isolated osteoderms are the elements most frequently preserved in the fossil record of the Cingulata, and therefore their external morphology has traditionally been the basis for most systematic schemes of this group (e.g. Ameghino 1897, 1902a,b; Simpson 1948; Scillato-Yané 1982; Carlini and

Scillato-Yané 1996; Carlini *et al.* 2002a,b,c, 2004, 2005a,b; Krmpotic *et al.* 2004, 2007a; Ciancio *et al.* 2005). The living representatives of the family are grouped in eight genera and 21 species (Wetzel 1985; Nowak 1999; Parera 2002). The extinct diversity is much higher, with nearly 40 extinct genera and 200 extinct species (Scillato-Yané 1980; Mones 1986; McKenna and Bell 1997).

According to McKenna and Bell (1997), the Dasypodidae are divided into three subfamilies: Dasypodinae, Euphractinae and Tolypeutinae. Dasypodinae contains the oldest representatives of the family, included in †Astegotheriini (Late Palaeocene–middle Miccene) (Bergqvist *et al.* 2004; Carlini *et al.* 1997, 2005b). This subfamily and the Euphractinae include most of the known species, both living and extinct. The Tolypeutinae are only recorded since the middle Miocene (*c.* 13 Ma) and did not attain significant diversity at any time (Carlini *et al.* 1997).

The species studied in the present work, *Chaetophractus villosus* (Desmarest 1804) Fitzinger 1871, belongs to Euphractinae (Euphractini), and occurs exclusively in the Neotropical region. The current distribution of *C. villosus* includes the Paraguayan Chaco, southern Bolivia, Argentina (extending latitudinally to southern Santa Cruz province) and southern Chile (from Bío Bío Region to Aísen Region) (Wetzel 1985; Redford and Eisenberg 1992); it has also been introduced in Isla Grande of Tierra del Fuego (Poljak *et al.* 2007).

Although the presence of osteoderms in xenarthrans is a unique feature among mammals, the first histological descriptions of osteoderms of *Chaetophractus villosus* were not made before 1931; at the time, the study was limited to pelvic buckler osteoderms and neglected those from the rest of the dorsal shield (Fernández 1931). Here we provide histological description and detailed comparative analysis of the osteoderms from the cephalic shield and the different body regions of the dorsal shield of *C. villosus*, based on serial histological sections. In addition, these descriptions are used as an empirical basis for the study and interpretation of the internal structure of osteoderms from fossil Euphractinae of the genus *Eutatus*, the last representatives of the extinct Eutatini, through application of palaeohistological techniques to serial sections of these materials.

We combined our data with previous work on *Dasypus novemcinctus* (Dasypodidae, Dasypodinae) (Cooper 1930; Hill 2006; Vickaryous and Hall 2006), to compare basic patterns of osteoderm histology in dasypodids, to contrast the morphological differences between the two most diverse subfamilies, which split at least 40 Ma (Delsuc *et al.* 2004).

The histological study of osteoderms of living dasypodids will allow deeper and better supported analyses and interpretations of osteoderm morphology in fossil dasypodids (Krmpotic *et al.* 2005). The fact that certain soft tissues are associated with distinct osteological structures provides a solid basis for the reconstruction of soft tissues in osteoderms of extinct dasypodids (Hill 2004, 2006). The orientation of colagen fibres governs that of hydroxyapatite crystals in bony tissue in many amniote clades (Scheyer and Sánchez-Villagra 2007). Precisely this biomineralization, which is preserved in fossil materials, allows reconstruction of the location of associated soft tissues lost during fossilization.

Materials and Methods

Histology

We dissected carapaces from three specimens of *Chaetophractus villosus* (adult individuals) that had been fixed in 10% formaldehyde. The carapaces studied were obtained from road-killed specimens of Buenos Aires Province (Bahía Samborombón), Argentina. These materials were deposited in the reference collection of the Vertebrate Palaeontology Department at Museo de La Plata. For each specimen, small portions of different carapace regions were decalcified (aproximately 10 osteoderms from each region). To evaluate different techniques, two decalcification processes were used: one set of osteoderms was treated with Bouin solution, and another was submerged in 8% nitric acid. Once decalcified, tissues were dehydrated using a 70% to 100% graduated ethanol series and embedded in paraffin. Osteoderms were cut into 5-μm thick longitudinal and cross serial sections. Sections were stained using haematoxylin and eosin, Masson trichrome and Periodic Acid–Schiff, to ensure visualization of most tissues. The histological slides are housed in the reference collection of the Vertebrate Palaeontology Department at Museo de La Plata.

Palaeohistology

For the analysis of fossil materials we used osteoderms from individuals of the extinct genus †*Eutatus* Gervais 1867 deposited in the collection of the Vertebrate Palaeontology Department at Museo de La Plata (MLP 69-IX-5-3). Osteoderms were mechanically prepared (for coarse fraction sediments) and by means of 100 volume hydrogen peroxide (1 : 10) (for fine fraction), to remove sediment from pores, foramina and cavities. Next they were embedded in coloured polyester resin and placed in a vacuum chamber to remove air bubbles. Once the resin solidified, preparations were sliced using a metallographic cutter and then polished with a metallographic grinding disc to obtain thin sections. Digital photographs were obtained every 150 μm and incorporated on a database for each osteoderm. The digital database is housed in the collection of the Vertebrate Palaeontology Department at Museo de La Plata added to the specimen number (MLP 69-IX-5-3).

Terminology

In describing the general morphology of osteoderms, researchers have used different terms to indicate the specific

structures. These terms are an improvement, but can become confusing, here we summarize the terminology used here and the equivalent used by other authors:

External and internal surfaces of the osteoderm = superficial and deep surfaces of the osteoderm (Hill 2006), external surface foramina = central perforations (Simpson 1948) or pits for hair follicle (Hill 2006), cranial portion = base (Holmes and Simpson 1931) and caudal portion = tongue (Holmes and Simpson 1931).

Results

External morphology of the carapace of Chaetophractus villosus

The carapace of *Chaetophractus villosus* (Fig. 1A) includes, from head to tail: cephalic or head shield, dorsal shield and caudal sheath. In turn, the dorsal shield comprises three movable nuchal bands, a scapular buckler, a region of movable bands (or rings) and a pelvic buckler. The dorsal shield comprises two major types of osteoderms: fixed osteoderms forming both bucklers (scapular and pelvic) and movable osteoderms arranged in rows forming the movable bands.

The external surface of fixed osteoderms is ornamented consisting of a central figure and several smaller peripheral figures (Figs 1B,C and 2A,B). All figures are convex and delimited by well-defined sulci. The central figure is elongated and occupies the posterior two-thirds of the osteoderm. The peripheral figures are located anterior and lateral to the central figure.

Surrounding the central figure there are foramina, which we name as external surface foramina. These are arranged at the intersections between the sulci between peripheral figures and the one surrounding the central figure. Some osteoderms also present foramina in the sulci between adjacent peripheral figures. The posterior margin of each osteoderm bears piliferous follicle foramina, from which emerge the hairs that partially cover the carapace.

At first glance the surface of the osteoderms is smooth, but under magnification (25 ×) it is seen to be rough by the presence of various small orifices and short meandering sulci. These structures correspond to the openings and courses of blood vessels and nerves situated below the epithelium forming the horny scales.

Movable osteoderms have two distinct regions (Figs 1C, 2B). The cranial portion is elevated, not exposed, lacking ornamentation, and occupies about the proximal one-third of the osteoderm. This area always lies under the caudal portion (the external surface) of osteoderms from the preceding row. The caudal portion overlaps the posteriorly adjacent osteoderm, comprising the remaining two-thirds of the osteoderm, and with the external surface ornamented similarly to the previous description for fixed osteoderms, i.e. one elongated central figure and smaller peripheral figures; however, in contrast with fixed osteoderms, normally only lateral peripherals are present.

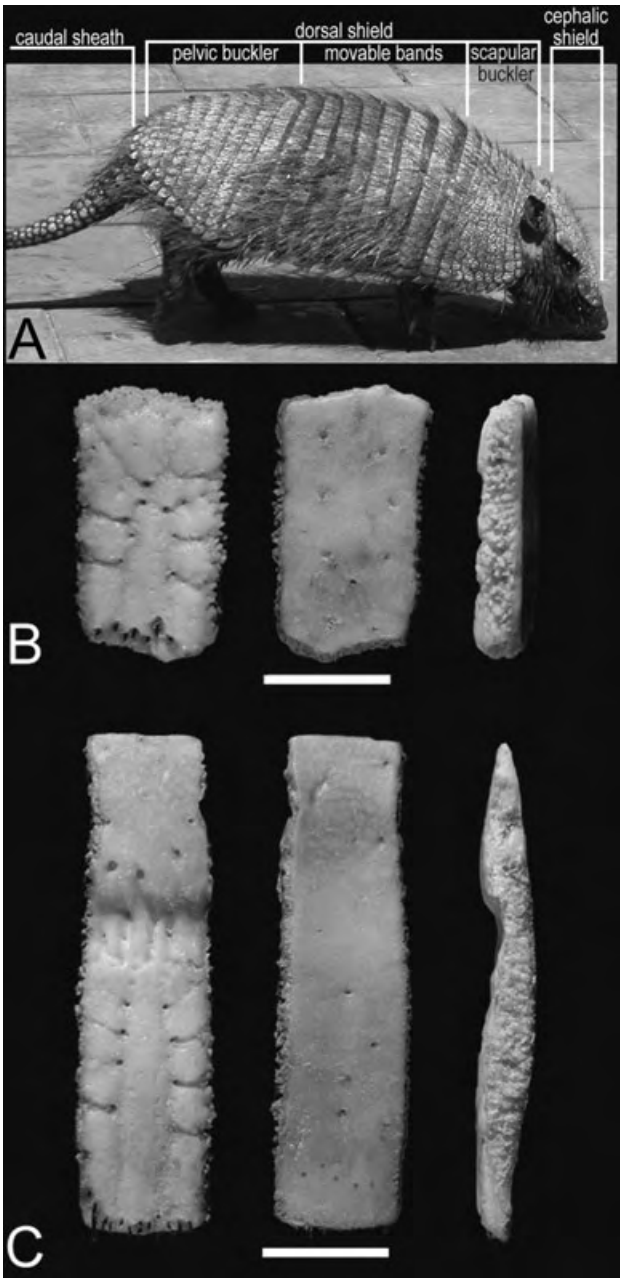

Fig. 1—*Chaetophractus villosus*. —**A**. Adult individual; —**B**. Fixed osteoderm from the dorsal shield; —**C**. Movable osteoderm from the dorsal shield; the osteoderms are viewed in external, internal and side views. Scale bar 5 mm.

A transverse depression with numerous longitudinal grooves that give it a 'striated' appearance is present between the cranial and caudal portions of the osteoderm.

The internal surface of each osteoderm (both fixed and movable) is relatively unmarked, with some irregularly distributed foramina that correspond to apertures for neurovascular bundles into the osteoderm.

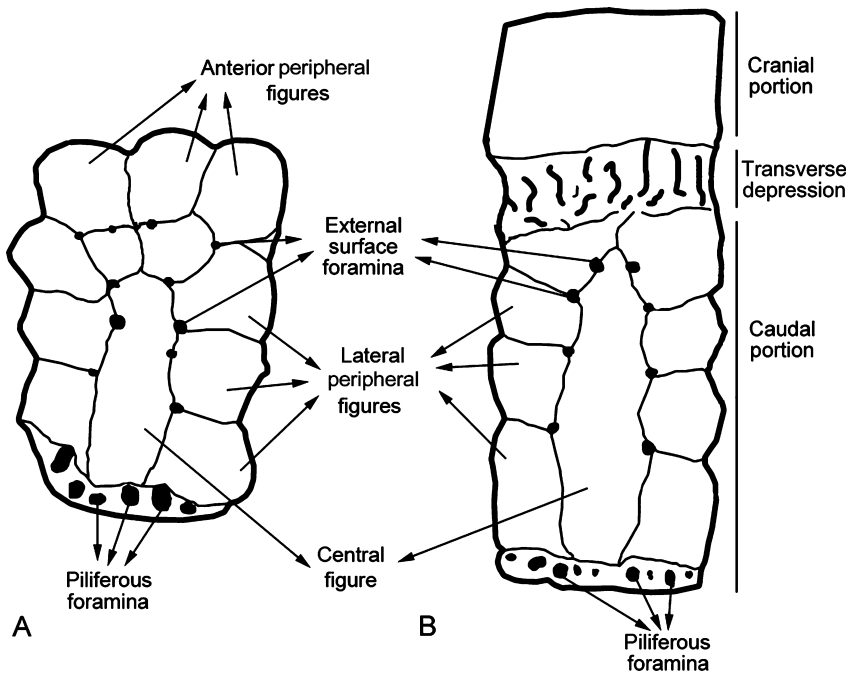

Fig. 2—*Chaetophractus villosus*. —**A**. Line drawing of fixed osteoderm from dorsal shield showing external structures mentioned in the text; —**B**. Line drawing of movable osteoderm from dorsal shield showing external structures mentioned in the text.

The previous description corresponds to typical osteoderms situated over the midline area of the dorsal shield. Towards the lateral margins of the shield osteoderms become modified and progressively asymmetrical. Marginal osteoderms are smooth, flattened and with a protruding posterolateral apex directed backwards; combined, these osteoderms are arranged in a series forming a serrated carapace margin.

Externally, each osteoderm from the cephalic and dorsal shields and from the caudal sheath is covered by an individual horny scale. This scale is thicker over the most prominent areas of the figures (both central and peripheral) and thinner at the sulci. In movable osteoderms the horny scale covers only the caudal portion, while the anterior region never has this type of cover and is only covered, in areas of greater mobility, by a smooth soft integument, not significantly cornified.

General histology of Chaetophractus villosus *osteoderms*

As commented above, we used two different techniques for decalcification of osteoderms. Bouin solution was slower (15–20 days), but better for maintaining structures and eliminating all calcium deposits; this technique was adequate for detailed description of tissues. The nitric acid solution was faster (4–5 days) but it required accurate time control, because excessive exposure can easily destroy the osteoderm; moreover, decalcification was not complete and the osteoderms often retained some small calcium deposits. This latter technique was useful for general descriptions.

Osteoderms of *C. villosus* are formed by compact bone. Longitudinal sections show three zones arranged in dorsoventral succession. The outer and inner zones are comparatively thin and formed by regular compact bone with primary and secondary osteons (Figs 3A,B and 4A,B). In contrast, the middle zone is thicker, representing about 50% of osteoderm thickness, and consists of bony lamellae arranged concentrically around large cavities. These cavities are filled mainly with adipose tissue, hair follicles, and sweat and sebaceous glands (Fig. 5). In a single osteoderm, from the cephalic shield, we identified elements corresponding to red bone marrow (Fig. 6).

Sebaceous and sweat glands are frequently encountered together, the former dorsally and the later more ventrally, within a single cavity. Both open into the external surface of the osteoderm by means of separate ducts that open at surface foramina (Fig. 7).

Distally, the osteoderm has several larger elongated and obliquely arranged cavities that hold the hair follicles (posterodorsal–proximoventral direction) (Fig. 3A). The proximal portion of these follicle cavities penetrates to the boundary inner zone, and the posteriomost portion opens dorsally on the posterior margin of the osteoderm, where hairs emerge through each of the hair foramina. Each hair follicle is occasionally associated with a sebaceous gland, or more rarely, a sweat gland. Cavities holding glands are generally located anterior to those that correspond to hair follicles, whereas those that do not contain glands or hair follicles are filled with adipose tissue. All cavities are connected by means of transverse tubes that correspond to Volkman's canals with blood vessels and nerves (Fig. 8). The outer zone has gland canals that open onto the external surface of the osteoderm, as well as small orifices for passage

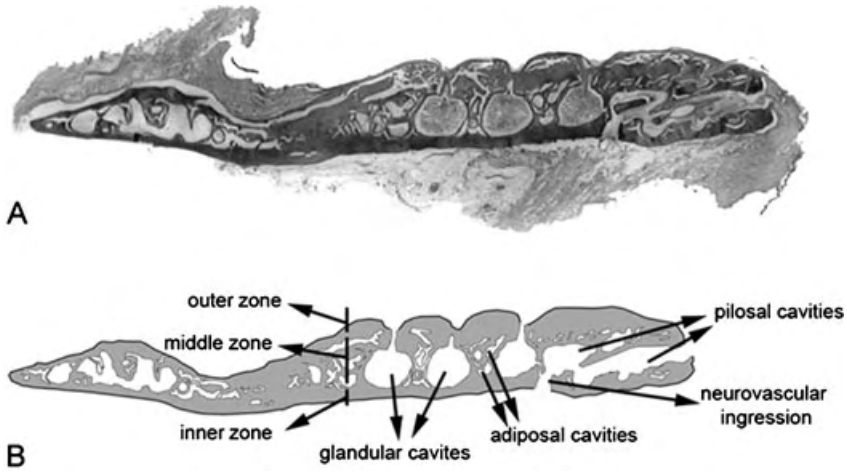

Fig. 3—*Chaetophractus villosus*. Movable osteoderm, longitudinal section (general view). —**A**. Histological section; —**B**. Representation of A, bone is in grey, and the general cavities occupied by soft tissues appear white. Arrows show the main tissues that occupy the cavities, and the three zones recognized in osteoderm section are marked.

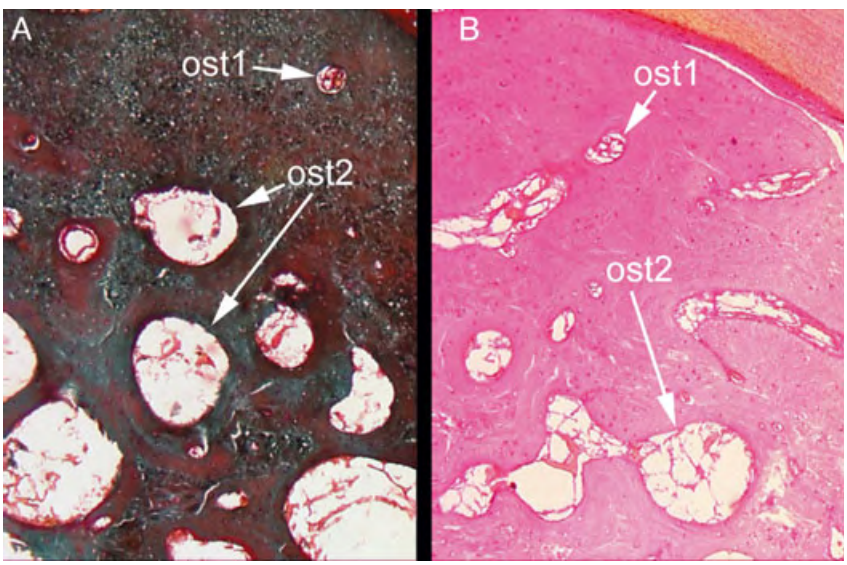

Fig. 4—*Chaetophractus villosus*. Histological details of pelvic shield osteoderms demostrating the primary and secodary osteon. —**A**. Trichromic stain 4 ×; —**B**. Haematoxylin & eosin 4 ×. ost1, primary osteon; ost2, secondary osteon.

of vessels and nerves toward the surface. Thin bundles of Sharpey's fibres, arranged perpendicularly to the long axis of the osteoderm, occur in this zone.

The inner zone also shows small canals for entrance of vessels and nerves into the osteoderm (Fig. 9A,B). This zone is much more collagen-rich than the external one; collagen forms thick bundles of Sharpey's fibres arranged obliquely to the greater axis of the osteoderm.

The surface of the lateral areas of contact between adjacent osteoderms is formed by numerous denticle-like projections interdigitating with those from neighbouring osteoderms. Adjacent osteoderm surfaces are joined by means of Sharpey's fibres between them that are thicker ventrally. In addition, at this level these fibres show a more regular arrangement that resembles that of the internal fibres of the osteoderm (Sharpey's fibres) (Fig. 10).

Histology and morphology of osteoderms from different regions

Cephalic shield. This element has a pear-shaped to subtriangular outline, covers most of the skull dorsally excluding the anterior half of the nasal region and has paired lateral notches at the level of the orbital region. Osteoderms of the middle and posterior regions of the shield are the largest, with ornamentation similar to that of the dorsal shield described above. The anterior marginals are smaller, lack ornamentation and although they vary in shape, are generally polygonal. Osteoderms of the cephalic shield are not arranged in distinct rows. Osteoderm cross-sections exhibit a poorly developed middle region, with up to three sweat glands and no sebaceous glands (Figs 11, 12). The posterior half of the osteoderm shows scarce hair follicles arranged as previously described. Occasionally, small, paired sebaceous

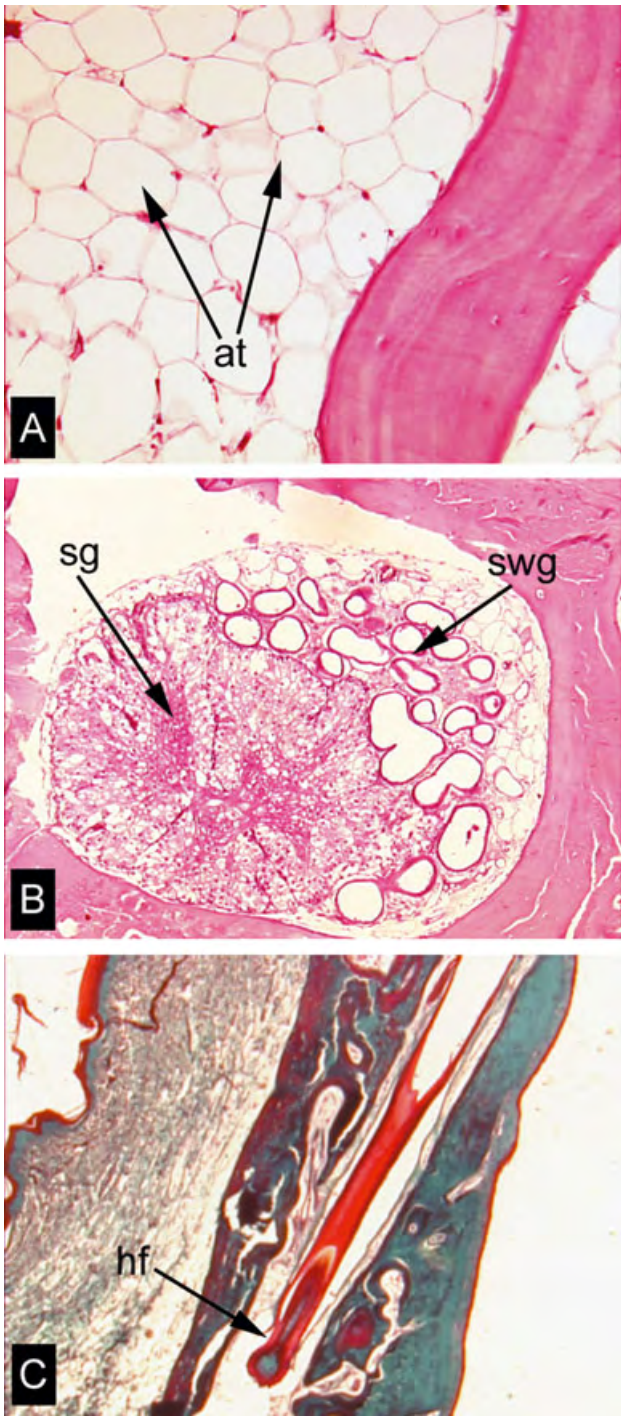

Fig. 5—*Chaetophractus villosus*. Histological sections of movable osteoderms. —**A**. Detail of adiposal cavity full of adipose tissue, haematoxylin & eosin (H&E) stain, 10 ×; —**B**. Detail of the arrangement of sebaceous and sweat glands in a glandular cavity, H&E stain 4 ×; —**C**. Detail of hair follicle, trichromic stain, 1.25 ×. at, adipose tissue; hf, hair follicle; sg, sebaceous gland; swg, sweat gland.

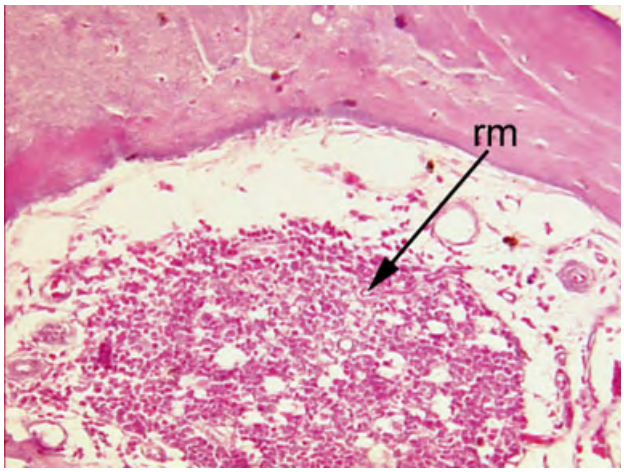

Fig. 6—*Chaetophractus villosus*. Histological section of cephalic shield osteoderm, details of red bone marrow, haematoxylin & eosin stain, 10 ×. rm, red bone marrow.

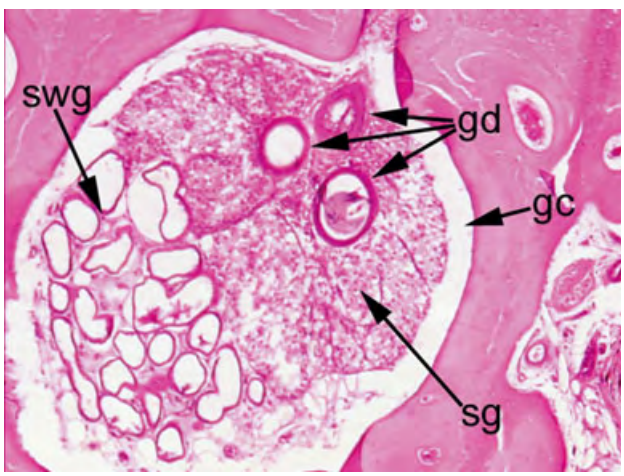

Fig. 7—*Chaetophractus villosus*. Histological details of a glandular cavity of movable osteoderm, containing sebaceous gland (dorsally) and sweat gland (ventrally). Haematoxylin & eosin stain, 4 ×. gc, gland cavity; gd, gland ducts; sg, dorsal sebaceous gland; swg, ventral sweat gland.

glands can be observed in association with one of the hair follicles.

Scapular buckler. This is the cranialmost section of the dorsal shield and covers the scapular region of the trunk. Five longitudinal rows of osteoderms are present medially, while laterally up to seven rows may be present. These osteoderms are mainly quadrangular and rectangular, although some are pentagonal in outline, especially in areas with multiple rows. The caudalmost row has the longest osteoderms; these are

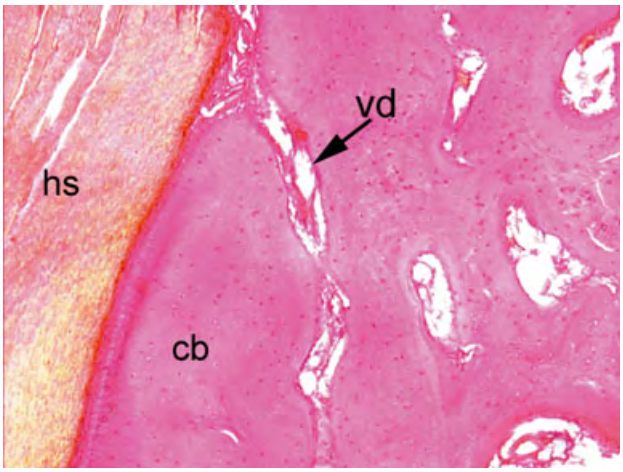

Fig. 8—*Chaetophractus villosus*. Section of outer zone of pelvic shield osteoderm shows details of a Volkman's canal, haematoxylin & eosin stain, 4 ×. cb, compact bone; hs, horny scale; vd, Volkman's canal.

rectangular and their ornamentation is similar to that of the osteoderm of the first movable band.

Cross-sections of osteoderms from this buckler show a middle zone comparable with that described above (Fig. 13). There are relatively more glands compared with the cephalic shield, and both sweat and sebaceous glands occur in each glandular cavity. Hair follicles are more numerous than in cephalic shield osteoderms.

Movable bands. This region comprises six to eight rows of movable osteoderms. The cranial portion of osteoderms from the first movable band lies below the last row of the scapular buckler, and the last movable band overlies the cranial portion of the first row of (semifixed) osteoderms of the pelvic buckler. The number of elements in each band ranges between 32 and 39.

Histological sections of these osteoderms show structural differences between the cranial and caudal portions. The cavities of the middle zone of the cranial portion contain only adipose tissue and neurovascular bundles, whereas the caudal portion of the osteoderm contains spherical cavities with glands (one sweat gland and two sebaceous glands per cavity). Cavities with hair follicles are located posteriorly to these glandular cavities. The general structure of the rest of the osteoderm is similar to the previous description (Fig. 3A).

Pelvic buckler. The pelvic buckler consists of about 10 rows over the sagittal plane. The first row is called semifixed because the osteoderms have a proximal cranial portion that is covered by the caudal portion of the last movable band, but in contrast to movable band osteoderms, the contact of the semifixed row with the next row is serrated. The remaining osteoderms of this region are fixed and rectangular, although becoming more isodiametric toward the margins. Marginal osteoderms are subtriangular. The number of peripheral figures around each central figure ranges mainly between 10 and 13. The number of osteoderms per row varies between 35 and 10 (in the latest row that demarcates the caudal notch). Hair follicles range between 2 and 12, more frequently four to eight (Table 1). The number of non-hair foramina on the external surface varies between 2 and 11, more frequently five to seven (Table 1). Frequently the third and fourth rows of the medial region of this shield include one to three (often two) osteoderms with large surface foramina (sometimes merged in a single foramen) at the level of the sagittal plane; these represent the openings of the pelvic glands. These structures are typical of many Euphractinae species (Fernández 1922; Estecondo *et al.* 1997, 1998, 1999).

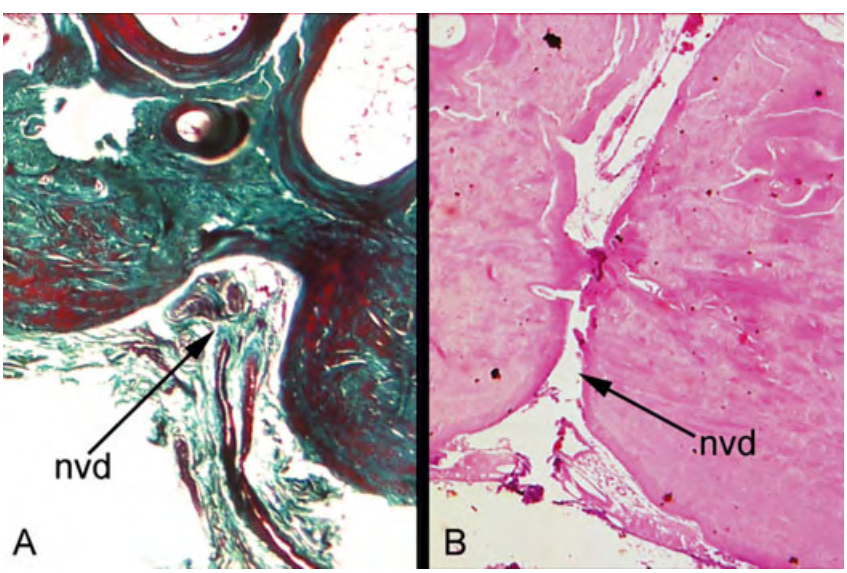

Fig. 9—*Chaetophractus villosus*. Histological details of an inner zone of movable osteoderms show neurovascular bundle entrance. —**A**. Trichromic stain 4 ×; —**B**. Haematoxylin & eosin stain, 4 ×. nvd, neurovascular bundle entrance.

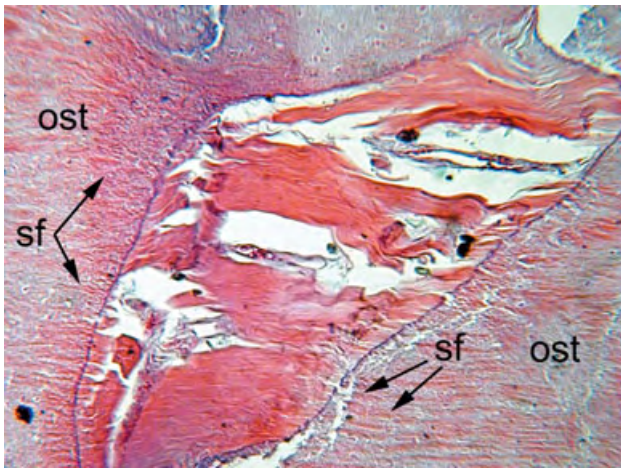

Fig. 10—*Chaetophractus villosus*. Histological details of a arrangement of Sharpey's fibres between two pelvic shield osteoderms, Periodic Acid–Schiff stain, 20 ×. ost, osteoderm; sf, Sharpey's fibres.

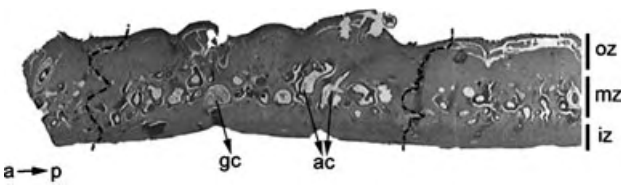

Fig. 11—*Chaetophractus villosus*. Histological section of cephalic shield osteoderms (general view) showing the poor development of the middle zone compared to osteoderms from other body regions. Dotted line pointed out the limits of a single osteoderm. a, anterior; ac, adiposal cavity; gc, glandular cavity; iz, inner zone; mz, middle zone; oz, outer zone; p, posterior.

Histological sections show the typical arrangement with three bone zones and some hair follicles posteriorly, associated with sweat glands. Histology of osteoderms of this region agrees with the general description (Fig. 14). Some sections show epidermal and dermal papillae, often accompanied by invaginations of bony tissue.

Table 1 Statistical data for number of external surface foramina and piliferous foramina for osteoderms of the pelvic buckler of *C. villosus*.

	External surface foramina		Piliferous foramina		
	Mean	Rank	Mean	Rank	Osteoderms (*n*)
Specimen 1	6.04	2–9	6.08	2–12	146
Specimen 2	6.30	2–11	6.56	4–10	164
Specimen 3	6.49	3–11	7.23	4–11	165

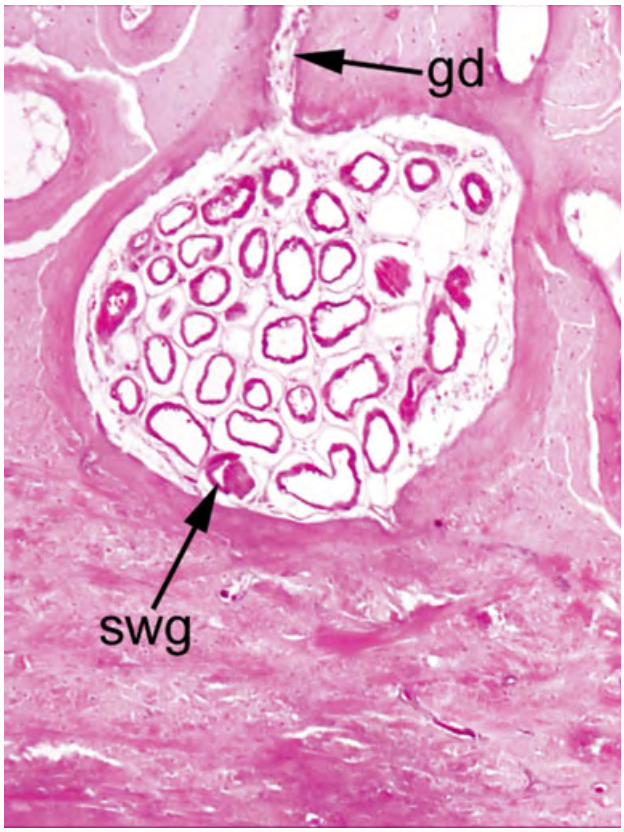

Fig. 12—*Chaetophractus villosus*. Histological section of cephalic shield osteoderm shows a glandular cavity occupied only by a sweat gland, haematoxylin & eosin stain, 4 ×. gd, gland duct: swg, sweat gland.

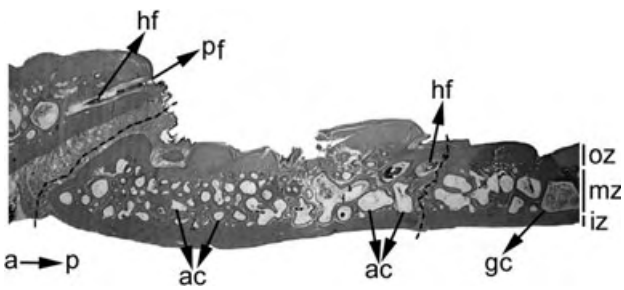

Fig. 13—*Chaetophractus villosus*. Histological section (general view) of scapular shield, showing the general internal arrangement of osteoderms and the well-developed middle zone compared to osteoderms from other body regions. Dotted line pointed out the limits of a single osteoderm. a, anterior; ac, adiposal cavity; gc, glandular cavity; hf, hair follicle; iz, inner zone; mz, middle zone; oz, outer zone; p, posterior; pf, piliferous foramen.

External and internal morphology of osteoderms of †Eutatus sp.

The osteoderms of *Eutatus* sp. have a rugose surface with numerous orifices (larger foramina and smaller punctuations)

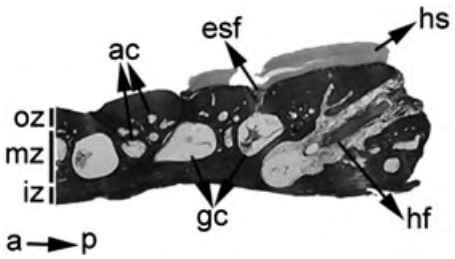

Fig. 14—*Chaetophractus villosus*. Histological section (general view) of pelvic shield osteoderm, showing the general internal arrangement of osteoderm. a, anterior; ac, adiposal cavity; esf, external surface foramina; gc, glandular cavity; hf, hair follicle; hs, horny scale; iz, inner zone; mz, middle zone; oz, outer zone; p, posterior.

and small furrows. Ornamentation of the external surface consists of a central figure delimited by peripheral figures (Figs 15, 16). The sulci delimiting the central figure do not reach the posterior margin of the osteoderm, so that the outline of the central figure becomes less distinct. The anterior half of the osteoderm demonstrated external surface foramina, located at the intersections of sulci between peripheral figures with the sulcus surrounding the central figure. A deep transverse furrow at the posterior margin of each osteoderm is divided by transverse septa that delimit a few large compartments. Since the first studies of eutatines (e.g. from classical works such as Burmeister 1883; Ameghino 1889, and later works), these have been attributed to hair follicle foramina (i.e. piliferous pits). The large size of these hair foramina has been cited as one of the most distinctive Eutatini characters. On the internal surface, the osteoderm surface is smooth, with various irregularly distributed perforations.

Palaeohistological sections of osteoderms from the midline of the pelvic buckler of *Eutatus* sp. specimens show the same three well-defined dorsoventral zones found in *C. villosus*: an outer zone formed by regular compact bone, a middle zone with bony lamellae arranged mainly around large cavities, and an inner zone also formed by regular compact bone (Fig. 17) that is diplöe-like (sensu Hill 2006). The middle zone forms up to 70% of the osteoderm thickness.

In addition to being traversed by larger canals coming from cavities in the middle zone, the outer zone is also pierced by small canals that branch and open as canals on the surface.

The middle zone contains spherical cavities that connect with foramina on the external surface by means of one or two canals.

There are also elongated cavities in oblique orientation (posterodorsal–anteroventral) with their anteriormost portion at the half of the osteoderm (generally surpassing the halfway line) or located even deeper in the inner zone, and with their posterior portion communicated with hair foramina. Lastly, irregular interconnected cavities appear in areas of the middle layer not occupied by these structures or glandular cavities. The inner zone is traversed by numerous canals extending toward the middle zone.

Discussion

The results of this work allowed clear identification of internal morphological differences between osteoderms of members of Dasypodinae and Euphractinae (see also Burmeister 1883 and Scillato-Yané 1982; for external morphological differences). As previously mentioned, these two are the major Dasypodidae clades and, according to all available evidence, split in the middle Eocene (more than 42 Ma) (see Carlini *et al*. 2002b, 2005b;

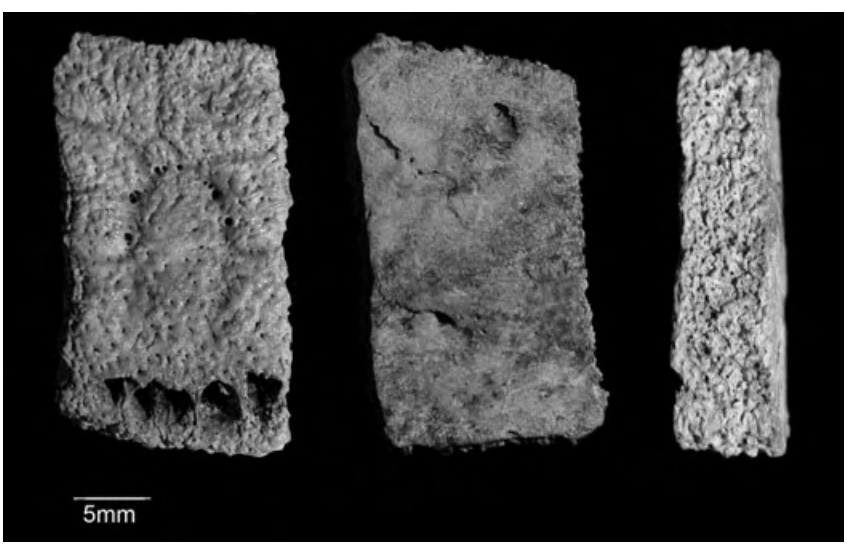

Fig. 15—*Eutatus* sp. (MLP 69-IX-5-3). Fixed osteoderm in external, ventral and lateral views (left to right).

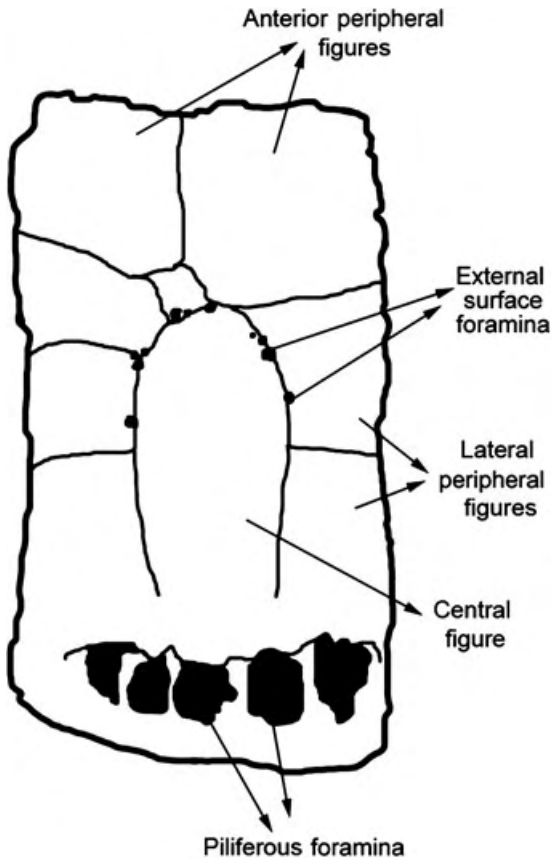

Fig. 16—*Eutatus* sp. (MLP 69-IX-5-3). Line drawing of fixed osteoderm showing external structures mentioned in the text.

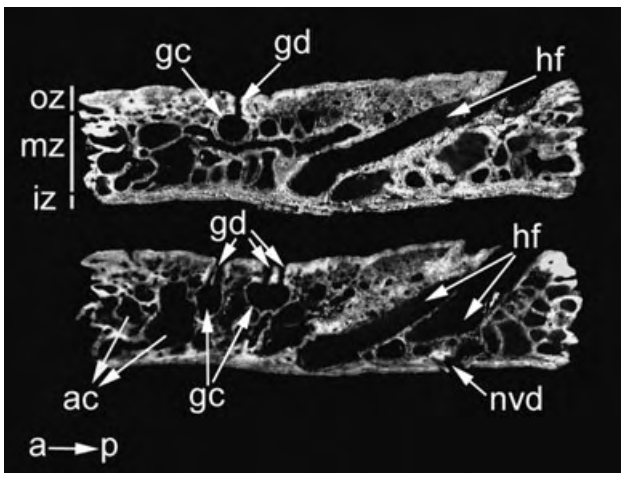

Fig. 17—*Eutatus* sp. (MLP 69-IX-5-3). Palaeohistological sections of fixed osteoderm, showing the general internal arrangement of osteoderms and the development of different zones recognized. a, anterior; ad, adiposal cavity; gc, gland cavity; gd, gland duct; hf, hair follicle cavity; iz, inner zone; mz, middle zone; nvd, neurovascular bundle entrance; oz, outer zone; p, posterior.

Delsuc *et al.* 2002, 2003, 2004). According to the recent and exhaustive works of Vickaryous and Hall (2006) and Hill (2006), and to our own observations (Ciancio *et al.* 2007), in Dasypodinae the middle layer is poorly developed and does not have cavities with adipose tissue. In *Dasypus novemcinctus*, the foramina of the external surface are not only associated with both types of glands, but also with hair follicles (Cooper 1930; Hill 2006; Vickaryous and Hall 2006), a condition not observed in *C. villosus* adults. However, Fernández (1931) noted that hair follicles develop in these cavities in *C. villosus* embryos, only to become atrophied during development (progenesis?). This condition supports the hypothesis that among dasypodids, the Euphractinae are more derived than the Dasypodinae (Carlini *et al.* 1997, 2005a), because they exhibit plesiomorphic features during their ontogeny that are not manifested in postnatal stages. Consequently, the presence of hairs associated with foramina on the dorsal surface of the osteoderm would be a plesiomorphic condition for dasypodids.

A middle zone with multiple cavities filled with adipose tissue does not occur in *D. novemcinctus* (we have not observed this condition in *Dasypus hybridus* either; see Ciancio *et al.* 2007), and such an association would only be present in the cranial portion of mobile osteoderms (see Cooper 1930; Vickaryous and Hall 2006; Hill 2006). Finally, Vickaryous and Hall (2006) identified red and yellow bone marrow in the osteoderms of *D. novemcinctus*, but we observed adipose tissue, possibly yellow bone marrow in the osteoderms and only found remains of red bone marrow in one cephalic shield osteoderm in *C. villosus*. The retention or loss of red marrow in osteoderms could also be of phylogenetic value.

Fernández (1931) hypothesized that the large amount of adipose tissue occurring in the middle zone of *C. villosus* could function as thermal insulation, or as a strategy to decrease shield weight. According to our analysis of *Eutatus*, the presence of a relatively larger middle zone would indicate greater amount of adipose tissue; this, together with the inferred development of hair, could be interpreted as an adaptation to colder climates like those that would have progressively developed during the Pleistocene (Zachos *et al.* 2001). Furthermore, we note that the osteoderms of both euphractines show great development of cavities that house adipose tissue, in contrast to the condition in Dasypodinae. Taking into account the known distribution of living representatives of both clades, we observe that the Dasypodinae are distributed in tropical to subtropical regions, whereas the Euphractinae occur from subtropical areas to cold temperate zones in the extreme south of the Southern Cone (Wetzel 1985; Redford and Eisenberg 1992; Parera 2002). Similar conclusions have been drawn about environmental requirements of extinct dasypodids, and the main cladogenetic events of the family have been compared with past marine temperatures, permitting a significant correlation between

temperature and relative diversity of the different groups (Carlini *et al*. 2005b and references therein). Lastly, the lack of significant differences between the middle zones of *D. novemcinctus* and †*Dasypus bellus*, given that the osteoderms of the latter are twice (or more) the size of those of the former (see Hill 2006) and three times that of small species (e.g. *D. hybridus*), lends additional support to the hypothesis that cross-sectional osteoderm structure is not necessarily correlated with body size. These data seem to reinforce the hypothesis that a plausible role of adipose tissue distributed within osteoderms is to serve as thermal insulation.

The study of osteoderms of living dasypodids allows us to propose homology hypotheses as well as make comparisons and interpret the structures preserved in osteoderms of extinct species, including the interpretation about the types of soft tissues that could be present in these elements. Thus, *Eutatus* sp. (Eutatini, Euphractinae) has cavities that continue as canals opening into foramina on the external surface that, according to the histological study of *C. villosus*, would correspond to glandular cavities and their respective canals. Similarly, it is probable that these cavities were occupied by more than one type of gland, because it is frequent to observe two canals issuing from a single cavity (Fig. 17). This arrangement is very similar to the condition observed in *C. villosus*, in which sweat and sebaceous glands share a single cavity and open via separate canals, in contrast to the description of Fernández (1931) who stated that both glands opened via a single duct.

The oblique cavities connecting with foramina on the posterior margin probably correspond to hair follicles. Contrasting with the condition in *C. villosus*, in *Eutatus* sp. more than one hair would exit through each hair foramen, given that up to three of these cavities can be observed opening onto the same foramen.

The remaining blind cavities (i.e. those that do not exit to the exterior) are inferred to have contained mostly adipose tissue. Lastly, the perforations observed both on the external surface and on the internal surface of the osteoderm would correspond to entrance and exit of neurovascular bundles, as observed in *C. villosus*.

General osteoderm structure in *Eutatus* sp. is very similar to that of *C. villosus*. This agrees with the hypothesis that these taxa are more closely related to each other than to representatives of Dasypodinae (Gaudin and Wible 2006). However, it may also be noted that the Eutatini and Euphractini show some differences within the basic Euphractinae pattern of internal structure of osteoderms (i.e. outer and inner zones, thin and formed by regular compact bone; and a middle zone, thicker and with large cavities surrond for bony lamellae concentrically arranged). In fact, the development of the middle zone is variable, and it has equal or greater relative development in *Eutatus* sp. than in *C. villosus*. The zone presumed to be the insertion area of hair follicles is more extended anteriorly in the osteoderms of *Eutatus* sp. On the other hand, each of the hair foramina of *C. villosus* communicates with a single cavity in which only one follicle is implanted, whereas the homologous foramina of *Eutatus* are much larger and communicate with several cavities that would probably have held more than one hair follicle; this would indicate greater pilosity than in *C. villosus*.

Final considerations

Osteoderms have always been the most frequent and abundant elements in the fossil record of Dasypodidae, and most extinct species are based on osteoderm morphology. However, it is noteworthy that relatively few characters from shield or osteoderm morphology have been included in most phylogenetic analyses of the group. Diverse phylogenetic analyses of Dasypodidae have included molecular data (Delsuc *et al*. 2002, 2003, 2004), and craniodental characters (see, e.g. Engelmann 1985; Gaudin and Wible 2006). In contrast, very few have included characters from the dorsal shield (Abrantes 2006), or integument (Hill 2005, 2006). Carlini *et al*. (1997) have partially proposed a phylogenetic scheme based on characters of osteoderms and dorsal carapace for both Glyptodontidae and Dasypodidae. The present study of osteoderm histology and morphology, together with those made by Hill (2006) and Vickaryous and Hall (2006), shows that the anatomical characteristics of these structures are also relevant for the study of relationships. Furthermore, it is consistent with previous hypotheses about the main cladogenetic event within the Dasypodidae. Lastly, there is remarkable agreement between the palaeoecological requirements of different groups of dasypodids inferred from non-skeletal data sources and osteoderm histology (Krmpotic *et al*. 2007a,b).

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ORIGINAL INVESTIGATION

Evolution of the axial skeleton in armadillos (Mammalia, Dasypodidae)

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Abstract

Intraspecific and interspecific variation in cervical, thoracic, and lumbar region of the vertebral column of Dasypodidae were examined in a phylogenetic framework. The number of vertebrae for each region were recorded for 86 specimens and metric data for each vertebra (centrum length, high, and width) were recorded for 72 specimens, including eight of the nine living genera. The number of vertebrae and degree of fusion between them were used to define four characters which were plotted on two alternative phylogenies of Dasypodidae. The ratio between centrum height and width is similar across all taxa analyzed except for Chlamyphorus, which exhibits a deviation in the last two lumbars. Tolypeutes matacus is unique among the taxa examined in having a second co-osified bone called postcervical bone, which is a fusion of the seventh cervical and first thoracic vertebrae. The thoraco-lumbar numbers of dasypodids are reduced when compared with other xenarthrans and are more diverse than those of some other mammalian clades of similar geological age and higher ecomorphological diversity. Changes in size are somewhat coupled with changes in the number of body segments. Independent of the phylogenetic framework taken, changes in size are accompanied with small changes in numbers of thoracolumbar vertebrae within each genus. There are functional and phylogenetic correlates for changes in number of thoraco-lumbar vertebrae in dasypodids.

Keywords: Vertebra; Modularity; Constraint; Phylogeny; Xenarthra

Introduction

The adult morphology of the vertebral column is an excellent proxy for embryological and molecular aspects of evolution, as the number of vertebrae is directly coupled with the number of somites; and the limits between regions of the vertebral column are coupled with boundaries in Hox gene expression domains (Burke et al. 1995; Richardson et al. 1998).

Different groups of vertebrates are known to posses distinct patterns of variation in vertebral count (Narita and Kuratani 2005). For example, it is well-known that mammals have a very stable number of cervical vertebrae, and pleiotropic effects of mutations leading to changes in this region are hypothesized to be coupled with this exceptional degree of conservatism when compared with any other group of tetrapods (Galis 1999). Certain changes in vertebral numbers are reportedly diagnostic of certain clades (Müller et al. 2008), such as an increase in thoraco-lumbar numbers in afrotherian mammals (Sánchez-Villagra et al. 2007) or less a reduction in the precaudal series count in trichechids (Buchholtz et al. 2007).

Among mammals, the xenarthran vertebral column is of particular interest for several reasons. The unique

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Table 1. Body size range and degree of fossoriality in dasypodids.

Taxon	Weight range (Kg)	Head-body length (mm)	Tail length (mm)	Total length (mm)	Degree of fossoriality
Zaedyus pichiy	1.25 - 2.35	277	124,8	401,8	Intermediate
Chlamyphorus truncatus	0.27 - 0.35	98,4	31,2	129,6	Very high
Calyptophractus retusus	–	75 - 140	35	–	Very high
Euphractus sexcinctus	3.00 - 6.50	395,7	220,2	616,4	Intermediate
Chaetophractus villosus	1.00 - 3.65	291,1	145,6	436,7	Intermediate
Chaetophractus vellerosus	0.26 - 1.33	–	–	376	Intermediate
Dasypus novemcinctus	2.00 - 6.50	–	–	645,7	Intermediate
Dasypus hybridus	1.09 - 2.04	–	–	459,5	Intermediate
Tolypeutes matacus	1.00 - 1.15	250,7	63,7	–	Low
Priodontes maximus	18.70 - 32.30	–	–	895,5	Intermediate
Cabassous tatouay	3.40 - 6.40	457,8	179	–	Very high
Cabassous chacoensis	–	300-306	90-96	–	No information

Data from Wetzel (1980), Redford and Eisenberg (1992) , and Nowak (1999) .

morphology of some articulations in the thoraco-lumbar region is the basis of the name 'Xenarthra' and a diagnostic feature to the clade (Gaudin 1999). The living sloths are among the very few mammals with a number of cervical vertebrae different than seven (Starck 1995 ; Buchholtz and Stepien 2009).

One of the three morphologically distinct living clades of xenarthrans are armadillos, the Dasypodidae. With a total of 9 living genera and 21 species (Gardner 2005), they exhibit a wide range of body size and degree of fossoriality (Table 1).

We examined the intraspecific and interspecific variability in the vertebral column of Dasypodidae and discuss these data in a phylogenetic and evolutionary framework.

Material and methods

We examined 86 adult and young adult specimens, recording vertebral counts for all of them and metric data for 72, distributed in 11 species (Table 2), and thus sampling eight of the nine living genera of Dasypodidae. Calyptophractus is the only one not included in this study. The materials are from the collections of the Museo de La Plata (MLP) and the Museo Argentino de Ciencias Naturales (MACN). Some specimens are from the personal collection of Alfredo A. Carlini (AAC) at the MLP.

Age classes were established according to the degree of fusion of the epiphysis from the vertebral centrum and the distal epiphysis of the femur as follows: adults, with both epiphyses of the vertebrae fused to the centrum and the distal epiphysis of the femur fused to the diaphysis; young adults, with vertebral epiphyses fused and distal epiphysis of the femur not completely fused; juveniles, with both vertebral and femur epiphysis unfused. The latter were not included in this study.

Only one specimen of Cabassous tatouay and one of C. chacoensis were examined and these data were supplemented with those obtained from a revision of the genus (Wetzel 1980). Because of access to mounted skeletons only, we were not able to collect metric data for Priodontes maximus. Skeletons that lacked the cervical region or few vertebrae of any region were used only if the position of the rest of the vertebrae could be identified. The only measured skeleton of Euphractus sexcinctus lacked the atlas hence the first vertebra was not taken into account in the analysis.

We examined the cervical, thoracic, and lumbar regions (Flower 1885) of the vertebral column. Sacral vertebrae are those attached to the pelvic girdle (or fused posteriorly to these vertebrae) and were not included in this study.

The variation in the number and fusions in some regions was used to define the four characters listed below, which were plotted onto two alternative phylogenies of the taxa examined.

Character 1: Fusion of cervical vertebrae: 0, fusion of second and third vertebrae; 1, fusion of second-fourth vertebrae; 2, fusion of second-fifth vertebrae.

Character 2: Postcervical bone (PC): 0, absent; 1, present.

Character 3: Number of thoracic vertebrae (TV): 0, nine; 1, ten; 2, eleven; 3, twelve; 4, thirteen.

Character 4: Number of lumbar vertebrae (LV): 0, two; 1, three; 2, four; 3, five.

Character 5: Number of thoracolumbar vertebrae (TLV): 0, thirteen; 1, fourteen; 2, fifteen; 3, sixteen.

Table 2. Dasypodids examined in this work.

Taxon	Identification number
Chaetophractus villosus	AAC-098, AAC-099, AAC-100, AAC-101, AAC-102, AAC-103, AAC-104, AAC-105, AAC-106, AAC-107, AAC-108, AAC-109, AAC-114, AAC-115, AAC-116, AAC-118, AAC-119, AAC-119, AAC-120, AAC-121, AAC-122, AAC-123, AAC-124, AAC-126, AAC-127, AAC-128, AAC-130, AAC-132, MLP-1214, MLP-819, MLP-795, MLP-15.X.98.03, MLP-821, MLP-855, MLP-918, MLP-785, MLP-922, MLP-831, MLP-860.
Chaetophractus vellerosus	AAC-134, MLP-18.XI.99.09, MLP-22.III.99.08, MLP-30.XII.02.69, MLP-30.XII.02.41.
Zedyus pichiy	AAC-110, AAC-112, AAC-113, AAC-117, AAC-131, MLP-9.XII.02.10, MLP-1210, MLP-1209, MLP-889, MLP-767, AAC-033, AAC-034, AAC-035, MACN-3.35.
Euphractus sexcinctus	MLP-1180, MACN-13.77.
Chlamyphorus truncatus	AAC-002, AAC-005, AAC-027.
Dasypus hybridus	AAC-111, AAC-125, AAC-129, AAC-133, MLP-5.IX.97.03, MLP-4.VIII.98.10, MLP-22.II.00.9, MLP-869, MLP-1211.
Dasypus novemcinctus	MLP-2.III.00.14, MLP-1215, MACN-17.105.
Tolypeutes matacus	MLP-13.XII.02.06, MLP-11.III.99.01, MLP-8.X.02.16, MLP-1217, AAC-013, AAC-014, MACN-29.908, MACN-17.112.
Cabassous tatouay	MLP-1183.
Cabassous chacoensis	AAC-060.
Priodontes maximus	MLP-S/N, MLP-1218.

The two phylogenetic topologies taken as a framework are Gaudin and Wible (2006, p. 160, Fig. 6.1) , based on a parsimony analysis of a comprehensive examination of 163 discrete cranio-dental characters and Delsuc et al. (2002, p. 1662, Fig. 3) based on a maximum likelihood analysis of data from the ADRA2B, BRCA1, and VWF genes. Chlamyphorus truncatus was not included in the analyses of Gaudin and Wible or Delsuc et al. The genus Chlamyphorus as used by Gaudin and Wible corresponds to a specimen of Chlamyphorus retusus, which following Gardner (2005) actually pertains to Calyptophractus retusus. The phylogeny of Gaudin and Wible (2006) differs from that of Delsuc et al. (2002) in the following aspects: First, in the hypothesis of Gaudin and Wible (2006) Tolypeutes is near the middle of a pectinate pattern and more derived than Priodontes and Cabassous, Delsuc et al. (2002) suggested instead thatTolypeutes is the sister-group of a Priodontes/Cabassous clade. Second, Gaudin and Wible (2006) presented Euphractus in a trichotomy with Chaetophractus and Zaedyus/Calyptophractus, whereas Delsuc et al. (2002) hypothesized that Euphractus is the sister-group of Zaedyus.

Characters were mapped onto the two phylogenetic topologies with Mesquite 2.5 (Maddison and Maddison 2008) and maximum parsimony criterion was assumed because it is the most common methodology used when the data source is morphological. Character 5 listed above is obviously not independent from characters 3 and 4, but it is useful to visualize the global changes in this region in dasypodid phylogeny. The character list we provide here is not expected to be uncritically incorporated in its totality in data matrices for phylogenetic analyses.

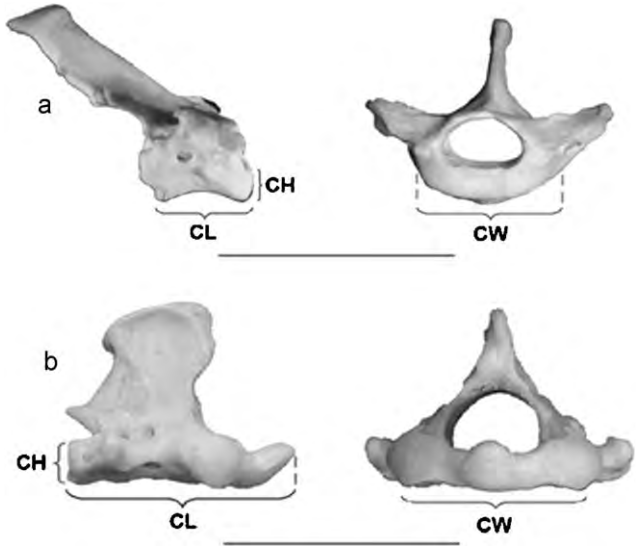

Fig. 1. Measurements taken from each presacral vertebrae of Dasypodids. (a) Measures taken for vertebrae from thoracic and lumbar regions. (b) Measures for vertebrae from cervical region. Abbreviations: CL ¼ Centrum length; CH ¼ Centrum height; CW ¼ Centrum width.

Three measurements were taken for each presacral vertebra examined (Fig. 1) using a caliper and recorded to the nearest 0.05 mm: centrum length (CL, measured ventrally), width (CW, measured ventrally) and height (CH, measured anteriorly except in cervical vertebrae that were measured posteriorly as shown in Fig. 1 a and b respectively). In the case of the fused cervical vertebrae (and a fusion between the last cervical and first thoracic recorded in three specimens of Tolypeutes matacus), we report for CL an average length for each vertebra based on a division of the total of the fused structure by the number of elements. Vertebrae in which measurements could not be taken were recorded as an average dimension between the immediately preceding and following vertebrae. For the others two measurements (CH and CW) the length recorded in the fused structure was the same for each conforming element.

Results

Fig. 2 summarizes the ranges in vertebral numbers in the taxa examined on the two alternative phylogenetic topologies considered, which also illustrate the hypothesized ancestral and terminal states in the characters examined. Although Chlamyphorus was not included in the phylogenetic analysis, the TV ranges between 11 and 12, the LV between 2 and 3, and the TLV are 14 in all specimens examined.

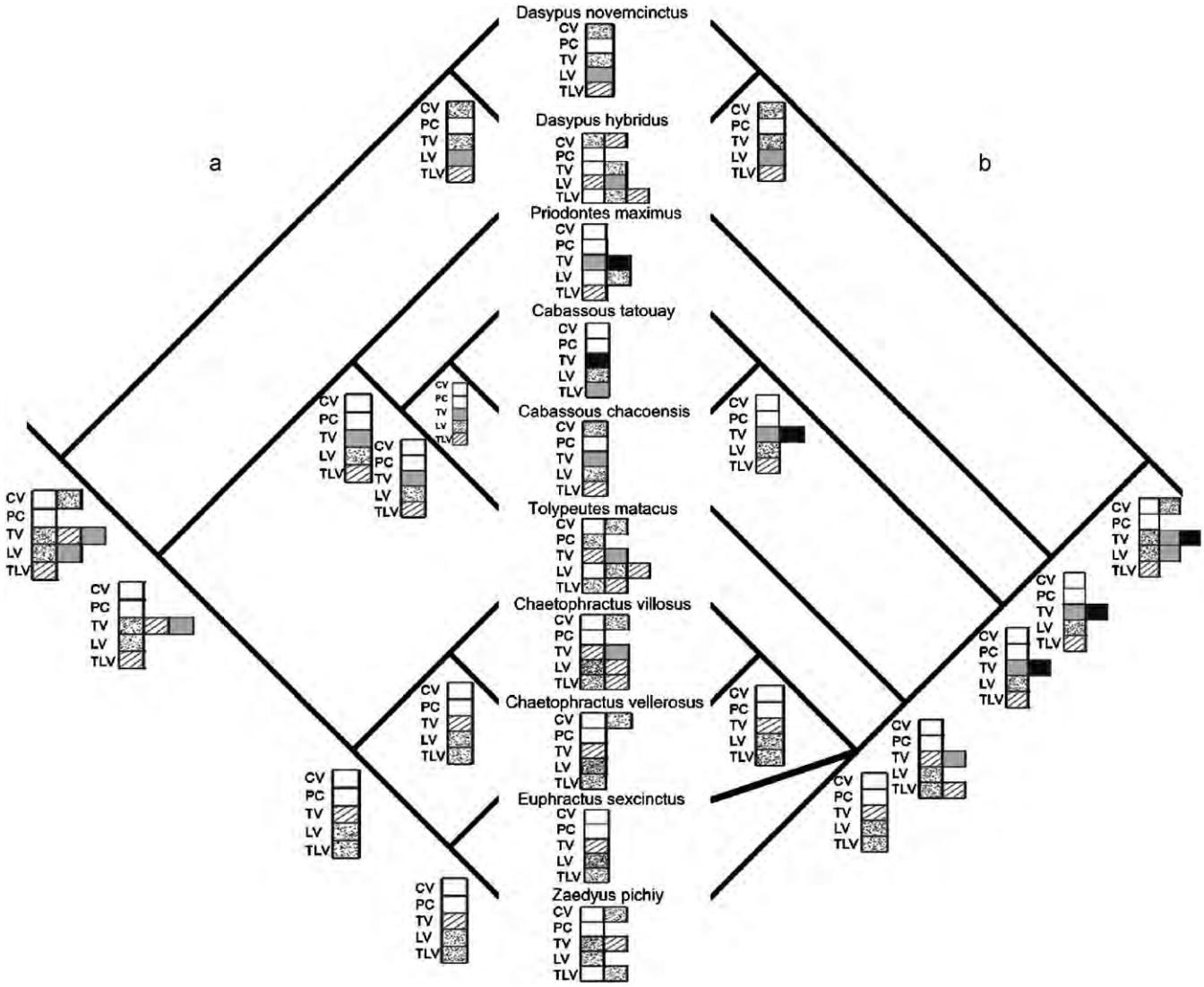

Fig. 2. Two alternatives phylogenies on which characters were plotted. (a) Delsuc et al. (2002) ; (b) Gaudin and Wible (2006) . Characters: CV ¼ number of fusioned cervical vertebrae; PC ¼ postcervical bone; TV ¼ number of thoracic vertebrae; LV ¼ number of lumbar vertebrae; TLV ¼ number of thoracolumbar vertebrae. States: White ¼ 0; Dotted ¼ 1; Diagonal stripes ¼ 2; Grey ¼ 3; Black ¼ 4. States references in text. Notice that more than one box for each character denotes a polymorphic condition for that species or node.

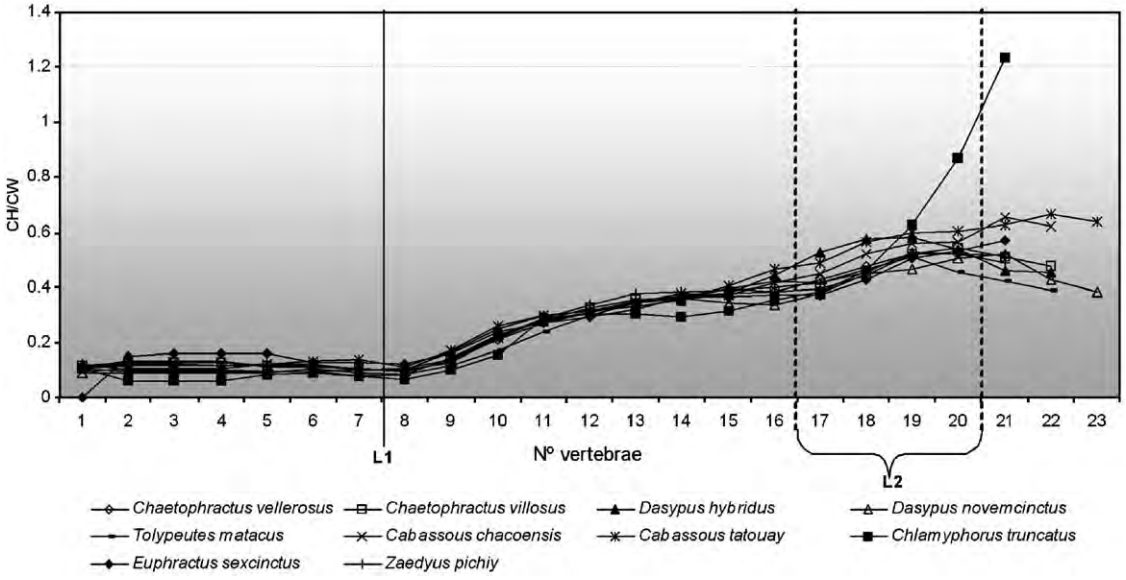

Fig. 3. Ratio between centrum width (CW) and centrum heigth (CH) of the presacral vertebrae for several Dasypodids. Abbreviations: L1 ¼ limit between cervical and thoracic region; L2 ¼ range limit between thoracic and lumbar region showing a highly variable position of this limit.

The ratio between height and width of the pre-sacral vertebrae best captures the morphometric variation we recorded here. This is illustrated in Fig. 3 for seven genera and ten species. The same general relations are found across all species with just one outlier in the lumbar region. In Chlamyphorus the last two lumbar vertebrae have a much larger ratio, even above one in the last lumbar, a unique condition among the armadillos examined.

As shown in Fig. 4 a, Chlamyphorus is the only armadillo examined in which the pelvic shield has a vertical orientation with respect to the vertebral column. The pelvic girdle is highly fused with this shield by several ischial bony extensions called fulcra (Atkinson 1870). This might be influencing the change in proportions between height and width of the lumbar vertebrae centrum.

Discussion

There is variation in the presacral region of dasypodids which is coupled with phylogenetic and functional changes in the group. The thoraco-lumbar numbers of dasypodids are more diverse than those of some other mammalian clades of similar geological age and higher ecomorphological diversity. Living carnivores, for example, almost always have 20 thoracolumbar vertebrae (Sánchez-Villagra et al. 2007). Whatever constraints are associated with this conservatism in carnivores (functional, developmental, etc.), this is much less evident in dasypodids. On the other hand, in the cervical region the number of elements remains constant among the different taxa examined but with a diverse scheme of fusion between the second vertebrae and the three that follow (Figs. 4 and 5 a), forming a co-ossified bone (Rose and Emry 1993) called mesocervical bone (Scillato-Yan e 1982). As shown in Fig. 4 b and 5b, Tolypeutes matacus is unique among the taxa examined in having a second co-ossified bone called postcervical bone, which is a fusion of the seventh cervical and first thoracic vertebrae, thus confirming what was reported by Scillato-Yan é (1982).

Some species exhibit more polymorphisms than others, as is the case of Dasypus hybridus when compared with D. novemcinctus Some states in that polymorphic condition are unique, as in characters 1 and 3. Some of the alternative methods of coding polymorphic states in character analyses (Wiens 2000) would result in the identification of an autapomorphy in some taxa, such as Dasypus novemcinctusin those two characters.

The number of vertebrae in armoured clades of tetrapods is less than that of their respective sister-groups (M üller et al. 2008). Turtles for example, have invariably 10 dorsal vertebrae. An extinct group of parareptiles, the placodonts, are also characterised by reduction in the number of dorsal vertebrae from around 20 in basal forms to 15–12 in armoured species. The same is found in dasypodids (Fig. 4) when compared to anteaters and sloths. The number of thoraco-lumbar vertebrae in the other two groups of Xenarthrans, Folivora and Vermilingua, is much larger than in armadillos, as exemplified by the following taxa: Choloepus 28 (Asher and Lehmann 2008), Scelidother-

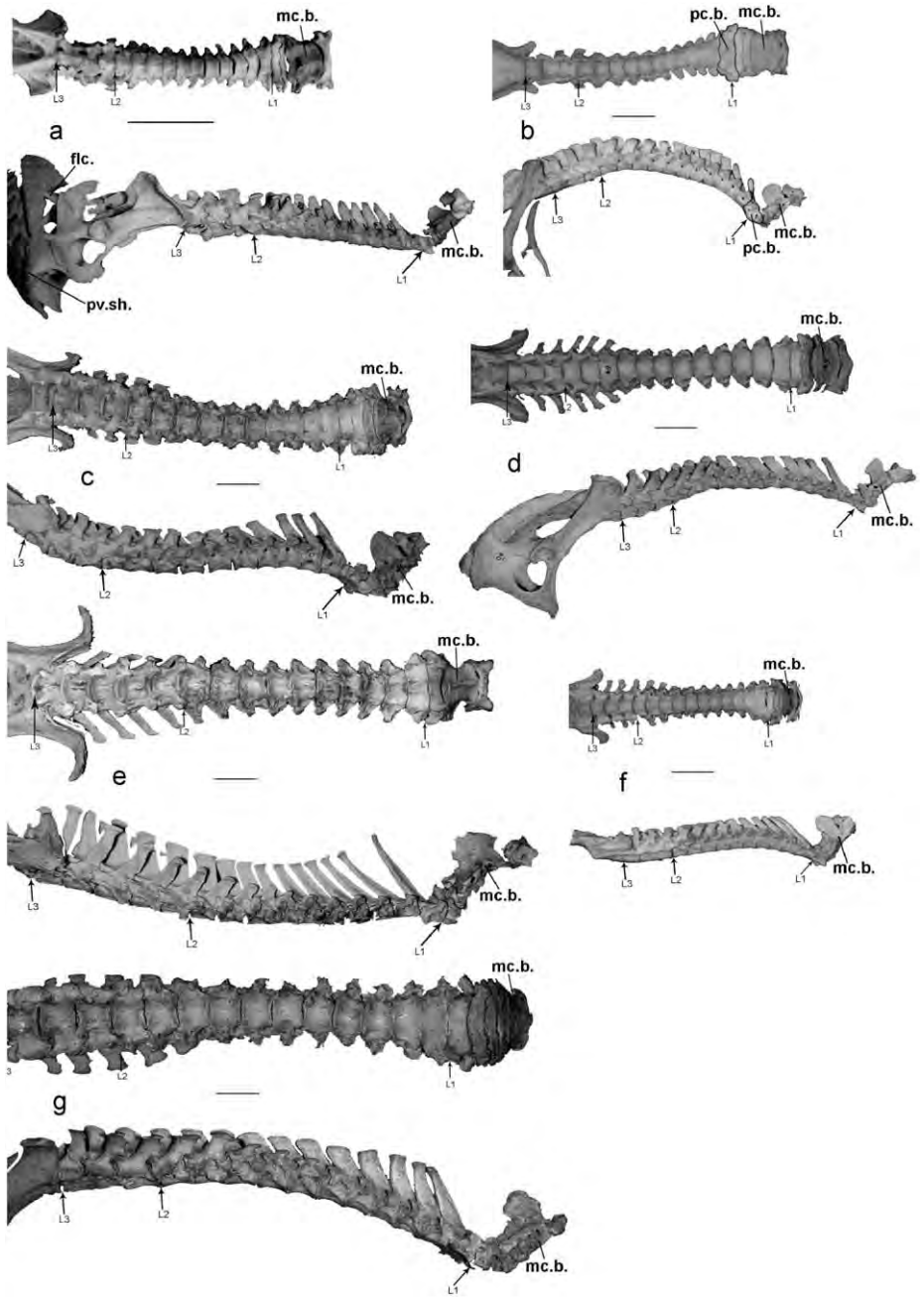

Fig. 4. Axial skeleton in dasypodids showing cervical, thoracic, and lumbar region. (a) Chlampyphorus (b) Tolypeutes (c) Chaetophractus (d) Cabassous (e) Dasypus (f) Zaedyus (g) Euphractus. Ventral view above each letter and lateral view below them. Scale bar ¼ 20 mm. Abbreviations: flc. ¼ ischial fulcra; L1 ¼ limit between cervical and thoracic region; L2 ¼ limit between thoracic and lumbar region; L3 ¼ limit between lumbar and sacral region; mc.b. ¼ mesocervical bone; pc.b. ¼ postcervical bone; pv.sh. ¼ pelvic shield.

ium leptocephala 20, Thalassocnus natans: 19, Megatherium americanum 19 (Sánchez-Villagra et al. 2007), Myrmecophaga trydactyla: 18, Tamandua tetradactyla: 19–20 (Jenkins 1970). A total of 19 thoraco-lumbar or more vertebrae appears to be the plesiomorphic condition for Theria and for the sister group of xenarthrans (Sánchez-Villagra et al. 2007), so there is no doubt that dasypodids have experienced a reduction in number. However, the presence of co-ossified bones in the neck is associated with digging habits (Rose and Emry 1993, and bibliography therein).

Considering the fossil record of dasypodids, we notice that the number of lumbar vertebrae found in Dasypus is congruent with that found in Stegotherium. Those genera are hypothesized to be sister groups by Gaudin and Wible (2006) . The number found in the euphrac-

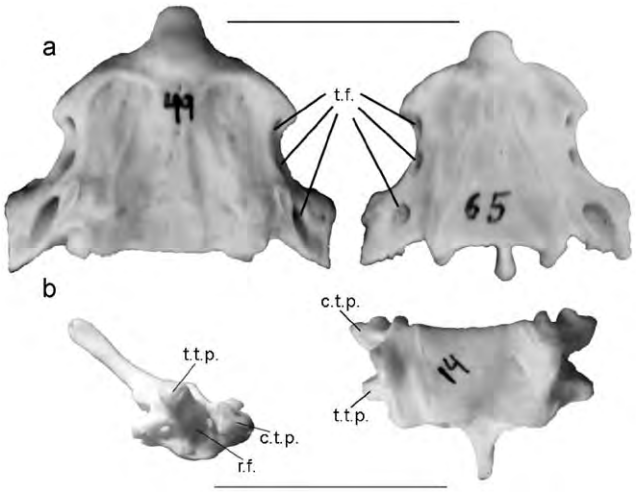

Fig. 5. Cervical fusion in Dasypodids. (a) Mesocervical bone in Chaetophractus (left) and Dasypus (right). The arrangement of the transverse foramina indicates the segmentary origin of this structure. (b) Postcervical bone in Tolypeutes. The bone has two transverse processes on each side, one from the cervical and another from the thoracic vertebrae. Scale bar ¼ 20 mm. Abbreviations: c.t.p. ¼ cervical transverse process; r.f. ¼ first rib facet; t.f. ¼ transverse foramina; t.t.p. ¼ thoracic transverse process.

tines Chaetophractus, Euphractus and Zaedyus are more similar to those of the fossil genus Proeutatus (Scott 1903–1905). This fossil is in a clade sister to the euphractines according to Gaudin and Wible (2006). A pattern also supporting the hypothesized position of these fossils is found for the thoracolumbar vertebrae, where Stegotherium has 15 TLV, similar to Dasypus, and Proeutatus has 14 TLV, similar to euphractines. This way there appears to be a reduction tendency in number of thoracolumbar vertebrae, in concordance with a more rigid carapace found in euphractines respect to dasypodines since the divergence of these two groups. This seems to support the fact that euphractines are more derived than dasypodines as it has already been suggested by Carlini et al. (2009) when examining the external ornamentation of the osteoderms in some Oligocene daypodids, and Krmpotic et al. (2009) based on an internal analysis of the osteoderms of some recent and fossil dasypodids.

The vertebral characters examined show more congruence with the phylogenetic tree of Gaudin and Wible (2006; see also Carlini and Scillato-Yané 1995), which is also true when one considers information from the fossil record. Tolypeutes posseses a combination of state characters from both the rest of tolypeutines and also from the euphractines, so a closer relationship with Priodontes/Cabassous clade is less well-supported than its pectinate position hypothesized by Gaudin and Wible (2006). The clade Chaetophractus/Euphractus/Zaedyus is well justified by all characters but a closer relationship between Zaedyus and Euphractus with respect to Chaetophractus cannot be resolved with the characters given.

Asher and Lehmann (2008) suggested that the relatively late eruption of the permanent dentition is a diagnostic feature of afrotherian mammals, which also show an increase of vertebral counts and absence of clavicle. These authors pointed out the similarity of this suite of evolutionary changes with a human genetic pathology called cleidocranial dysplasia (CCD), suggesting a potentially shared developmental basis for the evolution of these features. Dasypodids are characterized by derived dental features, such as the lack of enamel in adults (Starck 1995), but we are not aware of a special pattern or retarded dental eruption in this group (Martin 1916). Neither of these features which characterise afrotherians and the CCD condition are present in xenarthrans, as the clavicle is generally not reduced in this group (Starck 1995) and the number of thoracolumbar vertebrae is less than 19. This is relevant, as xenarthrans are depicted as sister-group of afrotherians in many recent comprehensive treatments of placental phylogeny (Springer and Murphy 2007).

When examining vertebral numbers, the extent of increase in somatic growth or segmentation has been of interest (Head and Polly 2007). In their review of amniote vertebral counts, Müller et al. (2008) concluded that there are no universal principles guiding the patterns of somitogenesis and that different kinds of constraints evolved independently within the different clades. In dasypodids, changes in size are somewhat coupled with changes in the number of body segments. Independent of the phylogenetic framework taken, changes in size are accompanied with small changes in ranges of thoracolumbar vertebrae within each genus (Fig. 2).

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